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Senses of the Sea

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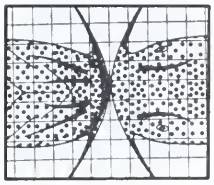

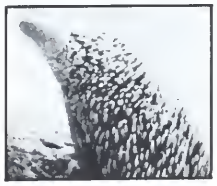

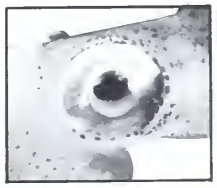

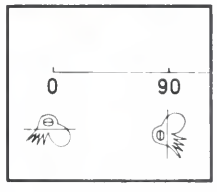

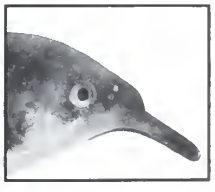

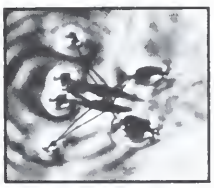

FRONT COVER: Octopus vulgaris. *The slit-like pupil of the octopus eye is always in a nearly horizontal position, regardless of the animal's position (see page 34). Photo by B.-U. Budelmann. BACK COVER: A bull shark. Sharks live in an electromagnetic sensory world (see page 55). Photo by Peter Stackpole, used with permission of* Life Magazine, © *1960, Time, Inc.*

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Senses of the Sea:

An Introduction

People perceive their environment within relatively narrow margins. This may sound small-minded to those who have highly individual and unusual views of the world, but, if we consider the possible sensory worlds as they are revealed to us through various animals, we begin to realize how *really* different the world might be for them: fishes "taste" distant objects with bodily sensors; porpoises identify objects by the way they reflect sound; bacteria are guided by small internal bar-magnets moving along the earth's magnetic field; and sharks locate hidden prey by the electric fields that all living bodies generate.

If the world looks so different to animals that have access to totally different sensory impressions, what, then, is the "real" world like? In a broader sense: what is the truth? This question lies, of course, at the heart of the natural sciences. What is accepted as reasonable proof for the existence of an object or a phenomenon is that one person can show it to another. In many branches of science, this proof has become indirect and relies on measuring instruments that "translate" the actual phenomenon into a perceptible form. For instance,

the electrical signals with which some fishes communicate are made audible to us via electrodes, amplifiers, and loudspeakers so that we can hear their electrical "voices." Thanks to this type of extended sensory equipment, we can attempt to form ideas of the worlds in which other animals live and we can give each other reasonable proof of the existence of those worlds. This issue of *Oceanus* is such an attempt.

Perception of our environment depends in large part on the stimuli that our specialized sense organs pick up and transmit to the brain. These stimuli — packages of chemical, mechanical, or electromagnetic energy — inform us of the state of the environment. Based on this information, we make conscious and unconscious decisions on how to proceed in the business of survival. Since we live on land and breathe air, we are exposed to typically terrestrial stimuli. Odors are carried by wind, we taste liquid solutions, and sounds are transmitted at 330 meters per second. The thin air medium allows electromagnetic waves to travel relatively unimpeded so that we can see the visible light spectrum in vivid colors and over great distances. Since air is a poor conductor for electricity, electrical stimuli are unknown.

The aquatic environment, in contrast, carries soluble chemicals via water currents to be smelled and tasted. Because of the greater density of water, sound travels here at 1,500 meters per second. The density of this medium and the various materials dissolved in it cause rapid absorption of electromagnetic energy that severely limits both the visible spectrum and the visual range underwater. Dissolved ionized material, however, increases the electrical conductivity of water and makes the transmission of electrical stimuli possible. Magnetic and tactile stimuli do not differ greatly in air or in water. Gravity is the same in both media.

The authors of this issue present examples of the special sensory adaptations aquatic animals have evolved to exploit their stimulus environment, maximizing their use of the stimuli that are critical for them. It is clear that each animal species specializes to meet its unique needs. Slow-crawling snails have a good set of chemical and tactile receptors, but only miniscule light organs for eyes and, as far as we know, no special hearing organ; their equilibrium receptor is a simple structure. (The eyes of the predatory snail, *Strombus dentatus*, are among the largest known in snails.) Fast-swimming sharks have developed almost every conceivable sense mechanism to great perfection: nose, eyes, equilibrium, touch receptors, electroreceptors, lateral-line organs for detection of water movements, and hearing.

In trying to imagine the entire underwater stimulus world and the sense organs that evolved to deal with it, one might lose track of the fact that each individual animal is a complete unit with several senses of different behavioral importance. When studying vision underwater a scientist selects animals with large eyes and well-developed visual brains. Another scientist studying hearing chooses animals whose hearing organs and acoustic behavior are prominent, and a third may choose a large-nosed animal to probe chemoreceptive capabilities. This situation leads automatically to exaggerations that obscure to some degree the fact that animals may simultaneously use different senses in their normal behavior.

One should thus keep in mind that these articles present dramatic examples of sensory capabilities in very diverse organisms. It should also be pointed out, however, that in some well-studied examples, senses are *not* used which may seem perfectly appropriate for the task. Catfish do not respond visually to lively swimming goldfish but hunt them down by using smell, lateral-line, and electroreceptor input. These same fish can use both smell and taste senses to detect amino acids, but they use smell, *not* taste, to establish a learned association between an amino acid stimulus and a novel behavior. It is thus well to remember that we need proper experimentation before we can assume that an animal uses one or another stimulus form or sense organ in a particular behavior. Perhaps some day an issue will appear in which the entire sensory world of a few animals can be presented.

Since for practical and historical reasons much basic knowledge of aquatic senses stems from research on freshwater animals, several examples are necessarily drawn from that environment. In some instances, such as in fishes that communicate with electrical signals, this may be largely or uniquely a freshwater situation. However, in most cases, the principles apply equally well to the marine situation. For this reason, we present these articles under the general title: Senses of the Sea.

Jelle Atema

A predatory snail, Strombus dentatus. *(Not to scale)*

Smelling and Tasting Underwater

by Jelle Atema

What Is in a Nose? To Smell or to Taste, That is the Question

A fish or lobster nose does not resemble a human nose. Yet, fish and lobster smell very well and, in many cases, far better than we do. In fact, smell and taste are as important in marine and freshwater organisms as they are in land-dwelling animals. These senses are based on receiving chemical stimuli from the environment; a process called chemoreception. The aquatic and the terrestrial environments, however, have different chemical stimuli and different ways of transporting and distributing them. Such differences have profoundly influenced both the appearance of receptors that receive the chemical stimuli and the mechanisms by which the stimuli are led to the receptors. All animals (both on land and underwater) need to analyze their

The lobster Homarus americanus. *(Photo by Linda Golder and Scrantz, MBL Photolab)*

chemical environment to locate food, shelter, and mates, and to avoid danger. And all animals must regulate their food intake and protect it from poisons. This has led to remarkable similarities that allow us to compare our nose with a shark or lobster nose. If we assume that life originated in the oceans, we may, in fact, expect that the noses of our fish-like ancestry made ours what they are today.

The Chemical Environment: Underwater and in Air

In a land environment, chemical compounds are in gas (volatile) form mixed in with the air we breathe. To us, that represents smell. In the aquatic environment, compounds are generally in solution (single molecules distributed among water molecules) or in suspension (small clusters or droplets of molecules floating in the water). We experience these only as taste, but aquatic animals can smell them as well. The physicochemical properties of the molecules determine how well they volatilize and how well they can be distributed in water or adsorbed onto surfaces to serve as useful biological stimuli. Amino acids, for instance, are soluble in water but have very little volatility; hence they can and do serve as aquatic chemical stimuli, but are useless as smell stimuli in air.

Amino acids are present in large amounts in the cells of all organisms, where they are involved in the synthesis of peptides and proteins. During digestion, proteins and peptides are broken down into amino acids again. Fishes and other animals can be viewed as leaky bags that slowly, through skin and gills, or in large pulses, through urine and feces, release various chemicals, including amino acids. These released chemicals form the animal's body odor, which can serve as a chemical picture of the animal that others can smell and identify as to species, sex, stress level, and perhaps size and individuality. Thus, it is not surprising to find that the ubiquitous amino acids are widely distributed in the aquatic environment, where they serve as indicators of biological activity. They can indicate the recent presence of a fish school, the density of plankton, or the fact that nearby a prey is being devoured or a carcass is rotting. As long as one has a sensitive amino acid detector, one can learn much about biological activity underwater. Several animals in salt and fresh water detect amino acids with much greater sensitivity than can our most sophisticated equipment.

Amino acids are relatively small molecules with molecular weights of a few hundred daltons* at most. Proteins can have molecular weights of a few hundred thousand daltons. Since they are soluble in water, they too, serve as chemical stimuli. One would expect protein detection to be useful to scavengers that live off dead and dying animals, whose blood and tissue proteins are set free after death and damage. Mud snails and lobsters, for example, have chemoreceptors for proteins. In the environment of air-breathing organisms, such large molecules occur only on rafts of small airborne particles, such as flakes of skin or pollen. Their use as chemical stimuli is unknown.

Chemical stimuli, both in air and in water, have some properties that distinguish them from other sensory stimuli, such as light, sound, or electricity. The latter have sources that can be located easily, whereas the location of chemical stimulus sources is difficult to determine. The source may move away, while the stimulus it produced lingers for a long time. Also, currents may carry the stimulus along complex paths of dilution, obscuring any kind of linear concentration gradient* that would allow us to determine the direction of the source. The distance to the source is even harder to detect. The "smoke-writing" of an airplane provides a good visual image of odor production and stimulus dilution in three dimensions. The airplane beautifully simulates a fish or school of shrimp leaving behind a fresh smell trail. Wind patterns soon create an unintelligible mass of little puffs of smoke. If these puffs were all we were given to locate the airplane, we easily might fail at the task; and if our food were airplanes, we would starve. Although truly linear concentration gradients could be created by diffusion, this process is extremely slow in water and requires the rare situation of a water mass without currents.

Chemical stimuli by and large are distributed by ever-present currents into volumes of water down-current or downstream from the source. The areas where the concentration of chemical stimuli is high enough that interested animals can be activated into responding are called active spaces. The linear gradient is an extreme and unusual case of active space. A situation roughly approaching a concentric linear gradient is the active space created by the release of an alarm substance in mud snails (Figure 1a). Trails are also specialized cases; in water they can be two- or three-dimensional. Two-dimensional trails laid on surfaces are common in both aquatic and terrestrial habitats. A trail can be followed to the source if one can detect its polarity to or from the source. Contrary to general belief, even highly trained and specially bred tracking dogs, such as bloodhounds, probably cannot determine the direction in which the trail is laid unless they compare the trail chemistry over a large distance. However, snails can perform the unlikely task directly upon encountering the trail (Figure 1b

*A dalton is a unit of molecular weight that expresses total mass and roughly indicates molecular size.

*In a linear concentration gradient, the number of molecules that is dissolved in water decreases evenly with distance from the source.

and 1c). Some marine shrimp follow three-dimensional trails in pursuit of food.

If the source cannot be easily located, why then do so many animals rely heavily on chemical stimuli for their survival? What has made chemical senses the most commonly used of all senses? Chemical stimuli are very good in some regards. They occur in large quantities, in dark or light, and they are highly specific yet require simple receptors. Many sources can be identified by a few specific chemical stimuli. The larger the stimulus molecule the more specificity it contains; even slight changes in molecular structure can serve to identify the source organism. Proteins are the ultimate in size and complexity. Mixtures of compounds can create an endless variety of stimuli, thus providing characteristic chemical pictures of the source that released them.

Filtering the Chemical Environment

It is thought that the receptors that identify a stimulus molecule are molecules themselves. The receptor molecule is probably a large protein that floats around in the membrane of the receptor cell together with many other receptor proteins. The receptors are constructed such that only certain stimulus molecules among the hundreds of thousands that are available in the environment can react with them. Thus they act as filters. In part because of the similarities found in chemoreception and immune reactions, there is much interest today in how a chemoreceptor cell distinguishes between different stimuli. For broad-spectrum cells, which respond to a wide variety of chemical stimuli, there are two possible explanations: either the receptor cell has many different receptor molecules in its membrane, each of which responds to one or a few related stimulus

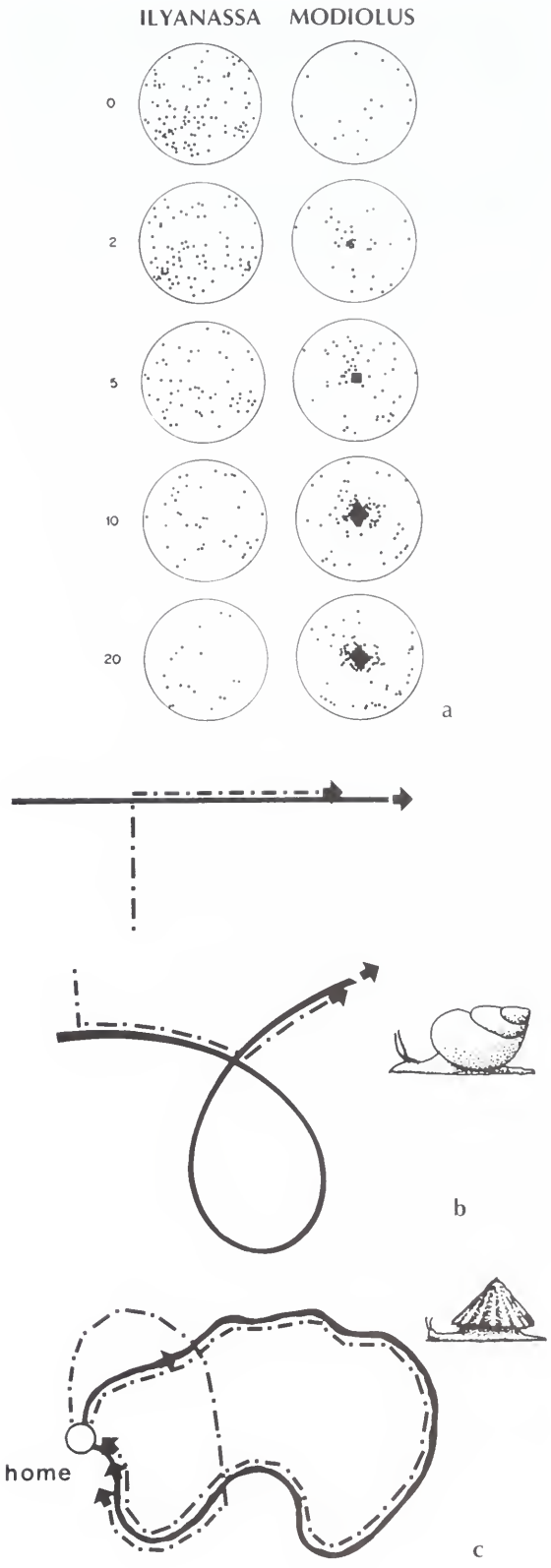

Figure 1. a)Responses of the mud snail Ilyanassa *to chemical stimuli released from a crushed snail of the same species (left column) and from a crushed mussel (right column). Each dot is one snail. The stimulus was introduced in the center of the circle at time 0 minutes. Numbers in the left margin show elapsed time. The mud snails bury themselves or move away when they smell the alarm substance released from another wounded mud snail; the area clears in a concentrically spreading circle. However, when a mussel* (Modiolus) *is crushed and placed on the mud, snails emerge from the mud and crawl "up the gradient" to areas of higher food stimulus concentration, eventually all collecting in the center to eat. The relatively even distribution of a chemical stimulus diluting away from the source is demonstrated in this active space (an area where, because of the high concentration of chemical stimuli, the animals respond). (From Atema and Burd, 1975). b) Snails commonly lay slime trails, another form of active space. They can follow (broken line) these trails chemically in the direction they were laid (solid line). (From Trott and Dimmock, 1978). c) Limpets follow their own trails to locate home – a spot on the rock they inhabit for long periods.*

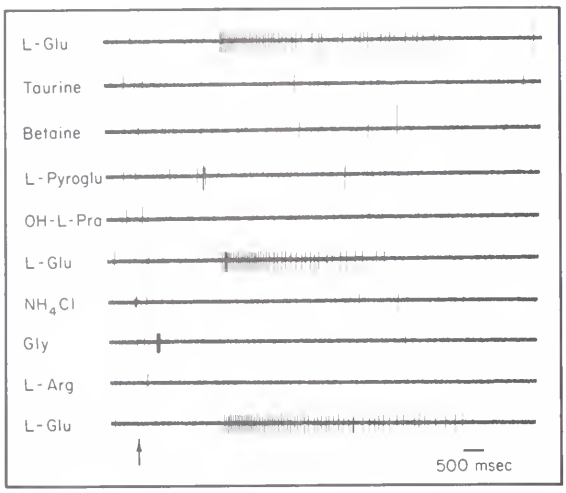

Figure 2. Coding for stimulus quantity in a narrow-band chemoreceptor: spike responses of one lobster taste receptor cell to L-glutamate. This cell type (located on the walking legs) responds far better to L-glutamate than to other compounds tested, even those which are very similar in chemical structure. The stronger the stimulus, the more spikes sent to the brain (in this instance, to the ganglia). (Courtesy of C. D. Derby)

molecules, or the cell membrane contains only one or a few different receptor molecules, each of which responds to many different stimulus molecules. The coded signals, called spike bursts, which these cells send to the brain, show that different chemical stimuli produce different bursting patterns in several receptor cells. With these coded signals, the brain can identify the stimuli, and thus the nature of their source.

To be useful in localizing the source, receptors must also be able to measure stimulus intensity, or at least relative concentration, to lead the animal toward higher concentrations. Coding for intensity is usually done according to the number of spikes in a bursting pattern: the more spikes, the stronger the stimulus. This effect is seen best in the narrow-spectrum receptor cells (Figure 2). These cells represent very narrow filters responding to only one or very few chemically related stimulus molecules. It is assumed that their membranes contain only one type of receptor molecule. Different animals have developed different specialized cells. The male silkworm moth, *Bombyx*, has an abundance of receptor cells that respond only to its own female sex attractant; lobsters have narrow-spectrum cells for particular amino acids presumably involved in feeding attraction. Although the information coding of narrow-spectrum cells is relatively easy to understand, that of the broad-spectrum cells continues to challenge us.

Bacteria respond to simple chemical stimuli, such as sugars or amino acids. They also can determine relative concentration. Their behavioral responses are simple avoidance or attraction. Higher animals have far more complex behavioral requirements for identifying, among other things, specific individuals, mates, food, home, or an enemy. Recognition of the necessary specific odor mixtures in an environment that is filled with chemical compounds requires a neural filtering network. First, the receptor cells filter out and identify individual molecules; then, the whole assembly of different receptor cells, aided by the brain, puts together a selected picture of the chemical world. Just as our visual system creates a typically human picture of the world, so can we imagine that the nose of a fish creates a chemical picture of its world, different from species to species and dependent on the many ways in which the environmental stimuli are filtered.

Experiments by William Carr at the University of Florida show that different fishes "see" different chemical pictures in the odor juices of the same prey. He presented the pigfish, *Orthopristis chrysopterus*, with chemical fractions of shrimp extract, particularly various amino acid mixtures. He found that only some of the extract's many amino acids were necessary in specific mixture ratios to elicit normal feeding behavior. Other amino acids apparently were not important, perhaps not even received by the animal. Thus, the pigfish seems to filter out most chemical stimuli in the environment and amplify the presence of a few. However, the pinfish, *Lagodon rhomboides*, selectively filters other amino acid mixtures out of the same prey extracts used for pigfish. Experiments with these and other fish species make it clear that the receptors and associated neural networks together act as selective filters limiting the animal's chemosensory world in a species-specific manner. This is comparable to the visual filters that fishes use to tune in on those features of their environment which are specifically important to them (see page 19). It also is illustrated by human experience: we do not see the ultraviolet that bees see or hear the ultrasound that bats hear.

One other filtering process is important. When we look for the proverbial needle in the haystack, it helps a great deal to know what that particular needle looks like; we need a visual search image. We form an image of the needle in our minds and search until we match this image with what we actually see: then we have found it. Do animals have images, thoughts? Are there chemical images, composed of scents, as well as visual search images? Or do animals have a complex filter that passively lets through only key odors?

Visual search images are known in birds. The example that initiated the idea of a chemical search image in animals is the behavior of tuna in Hawaii. Investigations on their chemical sensitivity show that this fish, which primarily relies on vision, not

only displays a high sensitivity to amino acids, but also can shift excitement toward different food odors. At first, the tuna were most excited by the body odor of a Hawaiian anchovy, but later, after feeding on a California anchovy species, they were more excited by the latter's odor. The odors differed in the relative amounts of amino acids and other compounds they contained.

Although we do not know the mechanism that causes this shift in excitement, it is possible that tuna form search images. Changing their hunting responses according to odors associated with recent food appears adaptive for tuna: when one prey species is abundant, it generally is abundant for awhile, and it usually pays off for the tuna to react strongly to that prey's odor. Eating it will further strengthen the response. In time, this prey species may become less abundant. Meanwhile, other prey may have greatly increased in numbers. The more the tuna feed on the new species the more their hunting will be stimulated by the new odor. Thus, the plasticity that is built into the chemical detection system, perhaps through shifting search images, appears highly adaptive.

We examined two other cases. The small pea crab, *Pinnotheres maculatus,* lives inside mussels, clams, or scallops. When removed from one host species and artificially placed with another, the pea crab began to show odor preferences for the new host. In feeding experiments with lobsters, *Homarus americanus,* we determined their chemical detection threshold for the body odor of two mussel species. The lobsters were then separated into two groups, each of which fed on one of the two mussel species. After a few weeks, the two groups of lobsters showed maximum sensitivity to the species odor they had fed on.

So far, we have discussed what the chemosensory world of aquatic animals may look like as it becomes filtered and amplified to suit the needs of different animal species. We have an idea of the molecular receptors and the plasticity of the processing mechanisms. But we have not yet described the great diversity of receptor organs, their specific functions and structures, and what ties together the chemoreceptor functions of so many diverse species, such as lobsters, fishes, and man.

The Chemoreceptor Organs

Human smell and taste are distinguished from each other by several criteria (Table 1). Whether other animals smell and taste depends on our definition of the terms. Since animals receive chemical information, we apply the term chemoreception to those which do not have a clearly distinguishable nose and tongue. The term is also used in the case of aquatic animals, where the distinction of air versus water falls away. However, I want to retain the concept of smell and taste for such animals as fishes, lobsters, and insects where a clear distinction of these two chemical senses can be made.

Smell and taste, then, must be defined by criteria that include both man and these animals. The last three criteria in Table 1 apply to all vertebrates — from fish and frog to lizard, bird, dog, and man; the last two apply not only to vertebrates, but also to most arthropods, such as crustacea and insects.

These last two criteria are closely connected: neuroanatomy, or brain structure, is the essential ingredient that gives sense organs their behavioral function, just as our leg and arm anatomy endows these extremities with different behavioral functions. The advantage of using the human concepts of smell and taste is twofold: it keeps language understandable for people who are not specialists, and it provides an impetus for studying the remarkable senses of smell and taste in other animals. From this we learn where we are uniquely human, where we have features in common with animals as far removed as fishes or lobsters, and possibly how and to what purpose our human senses evolved.

What is the experimental evidence for smell and taste in aquatic animals? The first two criteria in

Table 1. Criteria to distinguish between smell and taste.

Criterion	Smell	Taste
Organ	Nose	Tongue
Medium	Air	Water
Distance	Far	Close, contact
Threshold	Low (10^{-9} M)	High (10^{-2} M)
Spectrum	Broad (10^{4})	Narrow (4)
Receptor cells	Bipolar neurons, cilia	Taste buds, epidermal cells with microvilli
Neuroanatomy (brain)	Anterior brain, glomeruli, many connections to higher brain centers	Posterior brain, spatial projection, few connections
Behavior	Motivation, information, plasticity, search image (?)	Reflexes of food intake

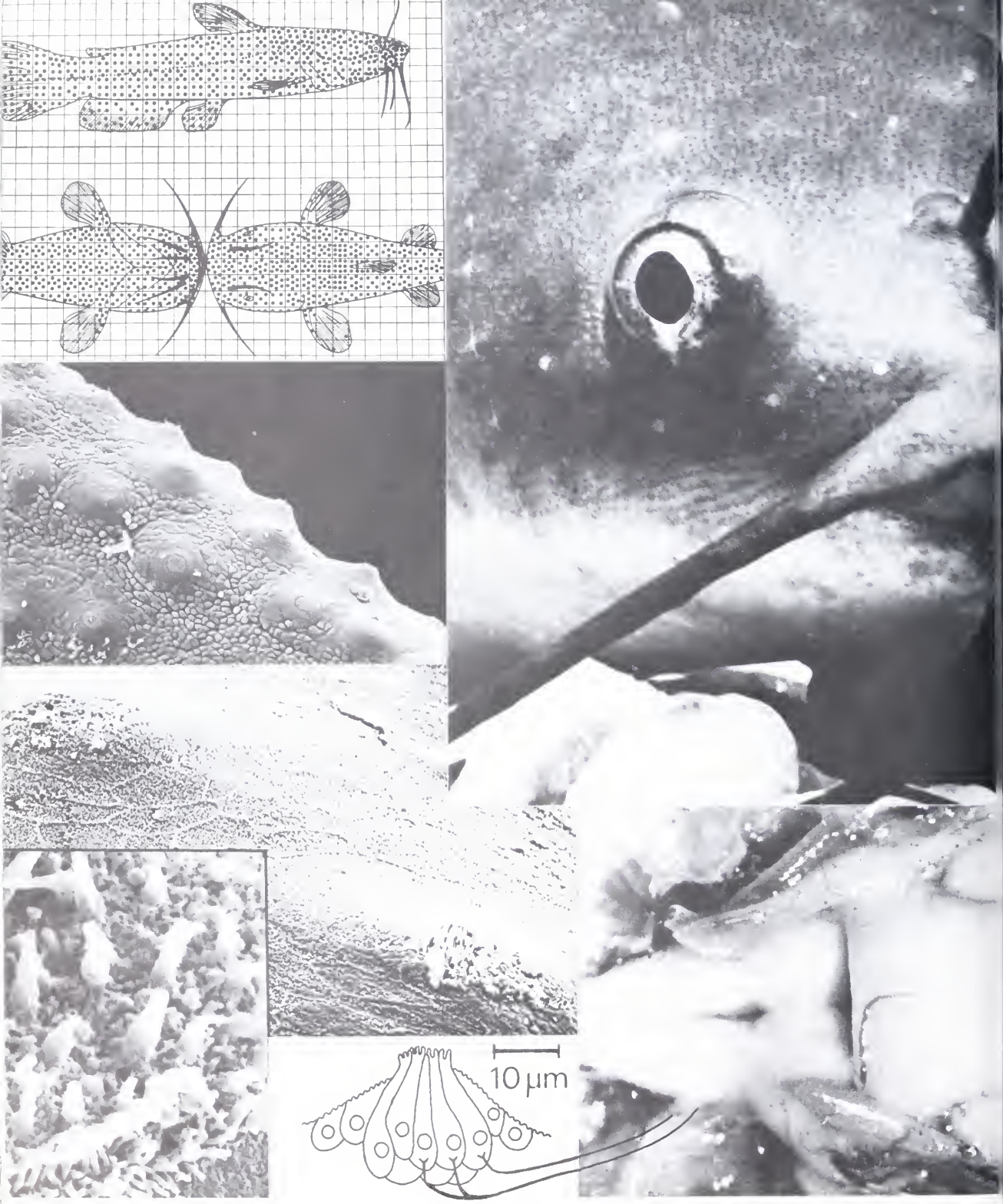

Figure 3. Catfish face with sensory apparatus. Small black dots on skin are pores in mucous leading to taste buds (TB). The nose (arrow indicates one of the two inflow openings) is located under and in front of nasal barbels. The white dots are openings to the lateral-line canal. Electroreceptors are distributed among taste buds in skin but are not visible here. Clockwise from top left: distribution of external taste buds (each dot equals 100 TBs); leading edge of lateral barbel with dense packing of TBs (over 100 per square millimeter); two TBs from roof of mouth (internal taste) showing microvilli from taste cells under the skin; enlargement of one TB; diagram of a TB cross section showing relationship of microvilli protruding from skin, round cluster of taste cells, and nerves connecting them to the vagal lobes of the

brain; dorsal view of brain with – from left to right – vagal lobes (internal taste), facial lobes (external taste), cerebellum (electroreception, hearing, lateral-line, and equilibrium), optic tecta (vision) which flank the cerebellum, forebrain (integration, "emotion"), and olfactory tracts leading to the olfactory bulbs; diagram of olfactory bulb and olfactory receptor cells with cilia; surface view of olfactory cilia (left) and motile cilia on surface of a lamella (which is a close-up of the pale square seen in the next photo); part of a lamella in the nose; catfish nose with lamellae. (Artwork by MBL Photolab)

Table 1 (organ and medium) clearly do not apply here. When we investigate the third, distance, we see that it does not apply either. Blinded catfish with plugged noses get as excited by a distant piece of meat upstream as do normal catfish with functional senses of sight and smell. We know also that catfish do not use vision to locate food, not even when it is as obvious to us as a lively goldfish; for live prey detection they use, besides chemical stimuli, water vibrations and electric fields (page 55). Even locating a source of food odor that is flowing from a hidden tube proceeds normally in the absence of smell. To determine if the sense of taste is really used by the animal in locating distant objects, we had to perform small brain lesions to eliminate taste sensation. It became clear that catfish have two separate senses of taste, one inside the mouth where the taste cells are connected to the vagal lobes of the brain and the other distributed over the entire body, especially dense on the barbels or whiskers (Figure 3). This external taste sense is connected to the facial lobes. Catfish with facial lobe lesions could no longer find pieces of meat or chow but still were able to successfully hunt for live fishes. Catfish with vagal lobe lesions found meat easily but did not swallow it. Apparently the external sense of taste makes the fish alert to the presence of food, guides the fish to the source, and triggers the suction reflex with which it picks up food from the bottom; whereas internal taste controls actual swallowing.

The separation of taste into two senses is not unique to catfish. Lobsters and other crustacea, as well as insects, have a sense of taste on their feet, equivalent to a catfish external taste sense, and another one on their mouth appendages, equivalent to catfish internal taste. In catfish, internal taste is more selective than external taste in accepting food: when a foul piece of meat is presented, a hungry catfish may locate it and even pick it up, but it will then spit it out. Pick-up and spit-out may be repeated several times. Apparently, what is accepted by external taste does not necessarily pass the more stringent approval of internal taste. Flies and lobsters show similar behavior. These and other experiments show that fishes, crustacea, and other aquatic animals use taste not only for testing food inside their mouths, but also for long-distance alerting and locating through their external taste sense.

To detect a chemical source far away, an animal must be able to measure very dilute stimuli, that is, it must have low-threshold detection. Thus, the criterion of distance is related to threshold (Table 1). It is generally assumed, based on human experience, that smell is more sensitive than taste. This is probably not true for many aquatic animals. Electrophysiological experiments have shown that catfish can detect single amino acids by smell and taste with equal sensitivity. The detection threshold found in these experiments is on the order of 10^{-9} molar.* For many human taste sensations we need a stimulus one million times stronger. Thresholds for lobsters were also determined by electrophysiological methods, and again amino acid thresholds for smell and taste were found to be similar, with a sensitivity matching that of catfish. Figure 4 shows the organs of smell and taste in the lobster.

Besides amino acids, many other compounds have been tested, among them amines, alcohols, sugars, and alkaloids such as caffeine and nicotine. This leads to discussion of criterion 5, spectrum. In analogy with vision and hearing where we speak of the visible and audible spectrum of wavelengths, we use the word spectrum in chemoreception to indicate all the molecules that surround an animal. Some of these molecules can be smelled, others can be tasted, and still others can be both smelled and tasted. Thus, an animal's chemically detectable spectrum for smell and taste overlap. Furthermore, the detectable spectrum varies among animals. For example, humans supposedly have only four tastes — salt, sour, sweet, and bitter — representing a very narrow spectrum, whereas many animals taste a far broader spectrum. For instance, they can distinguish between many different amino acids, proteins, peptides, and sugars, but we cannot.

The reason we separate human smell and taste by their spectra is that in contrast with taste, the sense of smell in humans can distinguish many thousands of different odors, singly and in mixtures. Many animals, both on land and underwater, have noses that match ours in terms of the breadth of detectable spectrum, although the individual compounds that make up the spectrum may differ greatly from species to species. Thus, in most animals, neither threshold nor spectrum criteria can be used to distinguish between smell and taste senses, which leaves the last three criteria — receptor cells, neuroanatomy, and behavior.

In all vertebrates, from fish to man, receptor cells for smell and taste are built very differently and serve as excellent criteria for identifying these senses (Figure 3). The sense of smell is built with specialized nerve cells, called bipolar neurons, which in one direction send branches containing the receptor proteins into the nasal cavity and in the other direction send branches carrying the coded sensory information directly to the brain. The vertebrate sense of taste is built with specialized epidermal cells that form clusters called taste buds sunken in the mucous membranes (for instance, on the tongue). All vertebrates have very similar taste buds in their taste organs, including both senses of taste in catfish. The taste cells have receptor

*M = molar: a solution of 1 M concentration contains 10^{24} molecules of that substance per liter of water; 10^{-9} M equals 10^{15} molecules per liter.

Figure 4. Chemoreceptor organs of the lobster, Homarus americanus. *a) Frontal view showing a pair of bifurcated antennules (smell) between the large antennae (tactile receptors), the walking legs with sensory hairs (tactile and chemosensory, equivalent to catfish external taste), and the maxillipeds (mouth parts with tactile and chemosensory hairs, equivalent to catfish internal taste). b) A scanning electron microscope photo of the underside of part of an antennule, showing two rows of aesthetasc hairs and several tactile guard hairs per segment. Other structures are also visible; their function is as yet unknown. c) The contents of one aesthetasc hair. Each hair is filled with the multiple processes of 400 chemoreceptor cells (only three are shown). Legend:* c = *cuticle;* n = *nucleus of supporting cell (sc);* ps = *proximal segment;* p = *pore;* m = *mitochondria;* mt = *microtubules;* r = *rootlets;* cj = *ciliary junction area;* ds = *distal segment. d) Walking leg with small claw bearing rows and clusters of sensory hairs. e) Enlargement of some of the presumed taste hairs. On right is close-up of one hair.*

proteins in their membranes, but they do not have the long branches found in smell receptor cells. Instead, the receptor membrane is folded to form microvilli where the cell is exposed to the external environment. To connect cell with brain, a group of special nerves comes down from the brain to receive the coded information of the taste cells.

We can only speculate why the structural differences between smell and taste came about. There may be both functional and historic reasons. The nose of vertebrates is not exposed to mechanical abuse. In man, as well as in all mammals, birds, reptiles, and amphibians, the receptor cells for smell are located deep within the nasal cavity. There, only air passes over the mucous layer in which the finest receptor cell branches are safely embedded. In fishes, the situation is only slightly different: water passes over a mucous membrane that lies folded up inside a special cavity. Their bipolar receptor cells for smell are very similar to our own. However, fishes' taste buds, which are located in the mouth and in other areas, undergo constant abrasion. Most animals are far less gentle than we are with what they put in their mouths. Some fishes pick up a mouthful of gravel and sort it out for food items, rejecting most of the inedible parts. Such rough treatment of the mucous layers of the mouth may make sunken taste-cell clusters necessary. Only small pores connect each taste bud to the inner surface of the mouth. Catfish and other fishes with external taste buds may suffer similar abrasive treatment on their skin. The delicate, long, and finely branched receptor cells of smell may not survive well in such an environment. This may be one explanation for the difference in smell and taste receptor structure in vertebrates.

There are many methods of packaging delicate receptor cells to protect them from

abrasion. In lobsters, smell and taste organs are built with similar bipolar receptor cells, but the fine hairs in which these cells are packaged are built very differently (Figure 4) and can serve to distinguish between smell and taste, as well as taste buds and bipolar neurons serve as criteria in vertebrates. In other words, for different groups of animals, there are different sets of receptor criteria for smell and taste. However, since insects and crustacea (but not vertebrates) have finely branched bipolar neurons as receptors for both smell and taste, the sixth criterion of receptor cell structure becomes invalid for generalization of the smell and taste concept beyond the vertebrates. The lobster's smell receptor cells are packaged densely inside fine, transparent, hair-like shafts. Each of these hairs (called aesthetasc hairs) contains the fine branches of about 400 receptor cells. The aesthetasc hairs stand in dense clusters surrounded by a row of protective guard hairs on the antennules, which make rapid flicking movements in the water around the head of the animal. Detailed and elegant experiments by Barry Ache of the University of Florida have shown that flicking is comparable to sniffing in mammals: it creates distinct impulses of odor stimulation in the patchy odor environment, thus aiding in localization behavior. As in a fish nose, serious mechanical abuse of aesthetasc hairs does not normally occur. In contrast, taste receptor cells are found inside stout, thick-walled hairs, which assume different shapes on different parts of the lobster's body. Figure 4 shows such hairs inside the small pincer claws of the walking legs of a lobster. The legs grab food and take it to the mouth; they also dig in sand and gravel, rip into mussels, and tear at plants. In short, this row of squat hairs suffers serious mechanical insult. The sharp spines of hard lobster shell material found on the exposed side of each hair may act as tiny teeth for tearing meat and also for protecting the delicate receptor cell branches inside against abrasion. It is clear that the receptor cells and the structures that contain them and allow access of stimuli are adapted to the micro-environment in which they must operate.

Adaptation to the environment may not be the only explanation for the unique vertebrate type of taste receptor cells. Another reason that vertebrates taste with epithelial receptor cells in taste buds and lobsters use hollow hairs with bipolar neurons is found in evolutionary history. Let us hypothesize that the evolution of the vertebrate taste system arose originally from bipolar neurons, whose receptor endings lie between the cells of the mouth and body skin and carry coded chemosensory information to the taste centers of the brain. Take the searobin, *Prionotus evolans* — it "walks" with the enlarged rays of its pectoral fins poking into the sand and mud bottom in search of food (Figure 5a). These specialized fin rays have numerous small bumps of skin cells, between each of which is a profusely branched nerve that carries detailed chemical information to centers in the spinal cord, not the brain. Everything looks like a typical fish taste system except that no taste buds are present. In addition to having an unusual spinal taste system, searobins have the normal fish taste-bud system in their mouth and on their lips.

Our hypothetical evolutionary scenario now calls for one change: a newly acquired capability specific to taste nerves from the brain allowing them to produce substances that induce ordinary skin cells to change into taste receptor cells. Two arguments support this. When existing taste nerves are cut, taste buds disappear; they return when the taste nerves grow back out to the skin. Furthermore, the hake, *Urophysis chuss,* has enlarged pelvic fin rays with which it pokes around (Figure 5b). These fin rays receive taste nerves from the brain as opposed to the searobin's spinal innervation — and in hake the fin rays are provided with taste buds! This shows that taste buds in the skin are indeed associated with special brain nerves. Thus, not only environment but also evolution may explain why vertebrates have taste buds.

Catfish, searobins, and hake not only present curious cases of taste superiority in aquatic animals, but they also illustrate a possible evolutionary pathway for the human sense of taste, and the important biological principle of historic restrictions on future evolutionary processes. In other words, now that vertebrates have a taste-bud system, they are "stuck with it" and in all likelihood will continue to perfect the system. They will probably never develop insect- or lobster-like receptor hairs. But they may already use a second taste system similar to the searobin's spinal taste: in all vertebrates, including man, various mucous skin areas, such as the nose, mouth, and eye cornea, contain free nerve endings that respond with remarkable sensitivity and precision to chemical stimuli. This poorly studied second taste system is known as the common chemical sense.

As described earlier, the receptor cells and their associated structures are adapted to the environment. The receptor cells are also physiologically adapted insofar as they contain receptor proteins for chemical stimuli that are found in the environment. And since these cells form the filters that link the environment to the animal's brain and behavior, they are also adapted to behavioral requirements. Charles Derby of the Marine Biological Laboratory at Woods Hole has found specialized glutamate receptor cells in the lobster, *Homarus americanus,* and Barry Ache has found specialized taurine cells in the spiny lobster, *Panulirus argus.* Both compounds can indicate the presence of meat or leaking body fluids, elicit feeding behavior, and indicate the nearness of food. Why the two species have specialized on

Figure 5. a) The pectoral fin rays of the searobin are connected to the spinal cord with spinal nerves that do not have properties that induce the formation of taste buds. b) The pelvic fin rays of the hake are connected to the brain with nerves that induce taste-bud formation in the skin, similar to catfish external taste. Despite these differences, both fishes use their fin rays in similar ways in probing the bottom for food. Both taste systems (with and without taste buds) are sensitive and complex chemoreceptors. (Photos by Russ Kinne, PR)

a

b

different food indicators is not known, but either stimulus would serve the purpose well. It may again be historic constraints, or just chance. Lobsters are active predators and thus interested in the odors emitted from live prey animals such as clams, snails, and worms. Such odors contain ammonia as a common waste product. It will not come as a surprise now to find frequent and sensitive ammonia receptor cells in lobsters. Catfish, as described earlier, also have sensitive amino acid receptors. They, however, seem to have focused on arginine as an especially important substance.

This leaves the last two criteria, brain and behavior, allowing us to apply the smell and taste concept to some invertebrates.

Brain and Behavior: Use of Chemoreceptors

We cannot completely understand a sensory system without knowing about its connections inside the brain. We must know how the animal "digests" the information provided by its receptor cells and how this information is used. Differences between smell and taste exist in all vertebrates and in some invertebrates. Again, catfish serve as good examples since much work has been done on them.

The smell receptors send their fine branches to a brain area called the olfactory bulb, where they make contact with a few different types of nerve cells. This area does indeed look like a small bulb, and it measures a few millimeters in diameter. The nerves inside the bulb form many fine clusters, called glomeruli, which are typical in the olfactory brain centers of vertebrates and arthropods. Although the nervous systems of these two major animal groups are in general completely different in organization, the olfactory "digestion" center is very similar. Thus, there must be something unique to this kind of brain organization for efficient analysis of the chemical environment through smell.

A large bundle of nerves leaves from the olfactory bulb to make contact with other brain areas. Thomas Finger at the Massachusetts Institute of Technology studied the brain connections of smell and taste in catfish. He found that each of the two olfactory bulbs is directly connected to a multitude of areas in the brain. Several of these areas are generally considered part of the limbic system. This section of the brain is associated, in catfish and man alike, with emotional behavior and motivation. The bulbs are also connected directly to each other and to an area in the hypothalamus; the latter is known (again, also in man) to regulate hormone balance. In other words, the sense of smell is directly connected to many of the higher brain centers regulating emotions, hormones, and motivation.

Catfish rely on smell for many of their

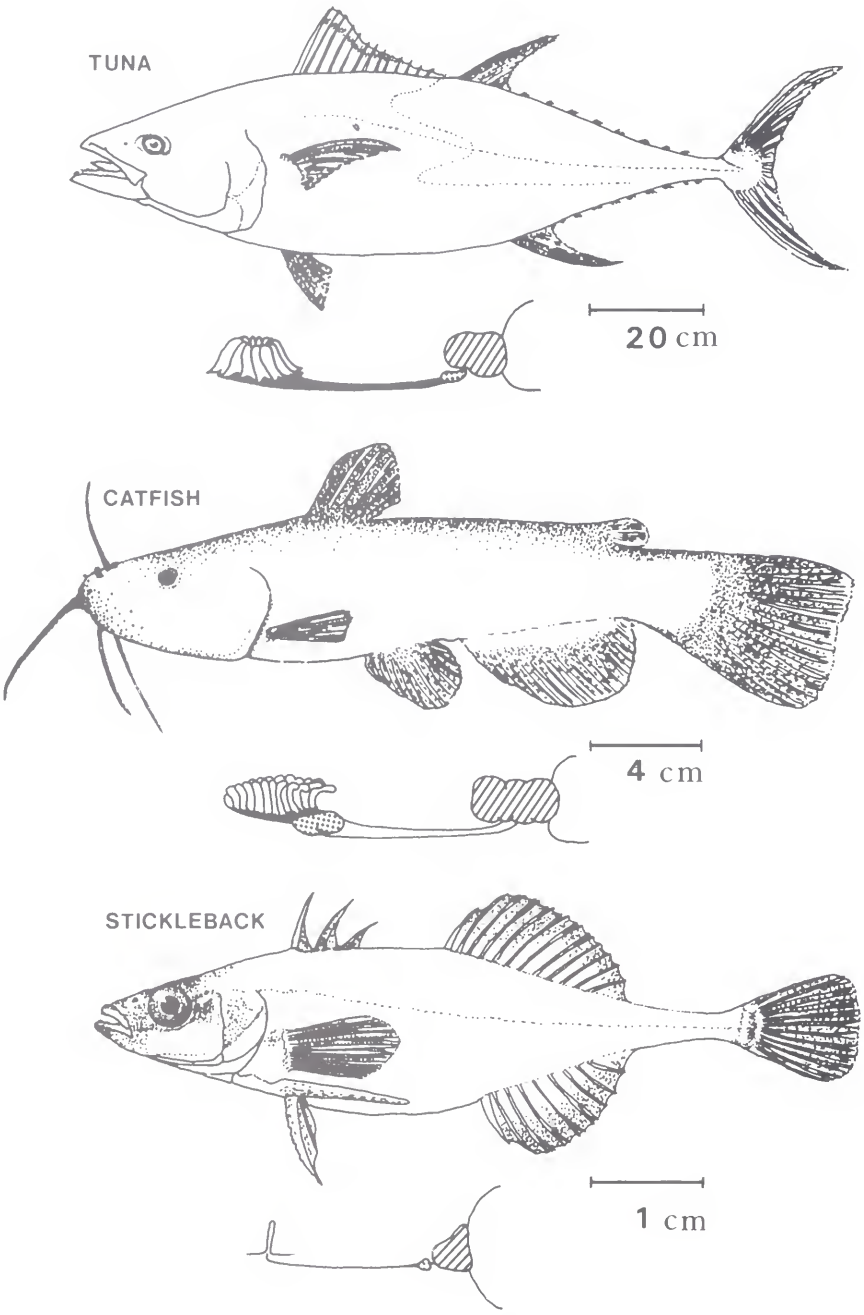

Figure 6. Size of the main components of the smell sense in three fishes. Note the relative size of their eyes. Under each fish is drawn its nose with the number of lamellae indicating the size and importance of the nose. From there a (black) nerve leads to the olfactory bulb (dotted) which is connected by a (white) nerve tract to the forebrain (hatched). Tuna have large eyes, a large nose, and small olfactory bulbs and tracts; catfish have small eyes, and large noses, bulbs, and tracts; sticklebacks have very large eyes, and very small noses, bulbs, and tracts.

behavioral needs. We can make an interesting speculation about smell in catfish and tuna. Both fishes have large receptor organs for smell, the real "nose" (Figure 6). Tuna are visual hunters that rely on smell only insofar as they need to detect the odors of their prey at a distance of many miles. Since this requires many sensitive receptors, their actual nose is large. Their olfactory bulb "digests" the information from the nose and notifies the rest of the brain that a particular prey odor has been detected. But this is perhaps the only simple message that needs to be transported: prey versus no prey. This may be why the tuna's olfactory tract, the nerve bundle going from the bulb to the brain, is very small compared to the one in catfish, where many different messages must be relayed. The large noses of both fishes allow sensitive detection of many chemical stimuli, but the kinds of behavior requiring smell input are far more complex in catfish than in tuna. Sticklebacks do not appear to

use olfaction very much; they have a very small nose (Figure 6).

The taste sense in catfish goes to two brain areas, where there are no glomeruli. From these areas a few large nerve tracts course through the brain and make connections to motor centers that control swimming and other behavioral reflexes. The paths through the brain are similar in all vertebrates. There is also a clear connection with the sense of touch and an indirect connection with the hypothalamus. In comparison with the architecture of the smell brain, that of the taste brain appears simple — with one unique feature. The taste buds in each body area of the catfish are connected to specific areas within the facial lobes. Areas with many taste buds, such as the barbels, occupy large brain areas; whereas the tail, for example, occupies a small area. A picture of a catfish as it is represented in its own taste brain shows enormous barbels, a small body, and tiny fins. This means (as can be easily demonstrated by touching a catfish body with chemical stimuli) that this fish knows its "taste space" as well as we know our "tactile space" (Figure 7). The taste senses of arthropods, such as lobsters, also are presumed to have rather direct connections to the nerves that control their muscles. In general, taste appears more as a reflex sense, simply stimulating certain behavior patterns, such as pick-up, swallow, and spit-out.

Smell, on the other hand, connects to many higher brain centers. When we plug a catfish nose or cut off a lobster's small antennae, we often see no change in behavior, or an unintelligible combination of effects. One must carefully design experiments to allow these animals to provide us with the answers we want: How and when is smell used? Why can't taste be used as well? What is so unique to smell that man, fish, and lobster have similar smell brains? Is this another case of convergent evolution (see page 34), as we see in the equilibrium organs and eyes of cephalopods and vertebrates?

This is one of the greatest unsolved questions we are faced with in our laboratory. We have found a few important things. There are substances that catfish can smell and taste with equal sensitivity (amino acids) and others they can smell better than taste (an alcohol compound). When we present alcohol in concentrations below the taste detection level but above the detection level for smell, we can train normal catfish to smell alcohol and be sure they do not also taste it. When we plug their noses, they can no longer smell and they no longer respond to the alcohol stimulus, even though the stimulus had been associated with food during training. But when we lesion their taste centers, the fish respond as if nothing has happened, even though such lesions are relatively major operations requiring anesthesia. When we train some fish to

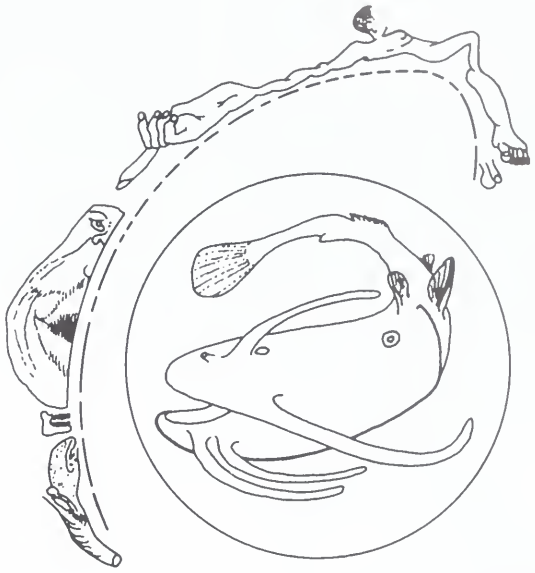

Figure 7. Sensory representation in the brain. Areas of great human touch sensitivity (cheeks, lips) are represented by relatively large areas in the brain. When, as here, body parts are drawn in proportions that signify their tactile importance, a tactile "homunculus" appears. (Early microscopists imagined homunculi, meaning "little men," in human sperm.) By analogy, a tasty ichthyunculus ("little fish") is drawn here with enormous barbels, a small body, and tiny fins. (Homunculus from Penfield and Rasmussen, The Cerebral Cortex of Man, *reprinted by permission of Macmillan Publishing Co., Inc., © 1950, renewed 1978 by Theodore Rasmussen. Ichthyunculus redrawn from Finger, 1976)*

the amino acid glutamine (which they can smell and taste with equal sensitivity) and then plug their noses, we get a first glimpse of what catfish use their noses for. Such nose-plugged fish no longer perform the learned task of going to the surface to get their food reward. Instead, they push their heads frantically against the tube that delivers the glutamine stimulus as soon as it is presented. It appears that they try to smell it, but they cannot, of course. This means that catfish perceive the glutamine stimulus very well (by taste) but no longer know what to do about it. They have learned with smell, not taste!

We can train catfish to recognize many different odors, to differentiate between male and female catfish odor, to tell individuals apart by odor, and to respond to one but not another amino acid. In each case, nose plugs cause the response to disappear immediately, and taste lesions do not make any difference. We cannot conclude that fishes do not learn with taste. Associations with bad- or good-tasting food can be made instantly by all vertebrates studied, including fishes. But nose-plugged catfish cannot be trained to perform the easy task of getting food at the surface even in three times the amount of time it takes to train a catfish with a functional nose.

Comparable information on the function of smell comes from salmon research. Salmon, in their

return to the home stream, remember the smell of water they lived in years before. The odor has been fixed in their memory during a sensitive period in the juvenile stage. Several years later, these fish (and other homing fishes) can use this memory and select their own stream odor from among many others. Without a nose, they lose this ability. This impressive behavior is also reminiscent of search-image filtering, as discussed earlier. Perhaps the nose provides fishes with a flexible, plastic filter with which powerful associations can be made. In salmon, the filter stays intact for several years; in tuna, the odor filter changes with prey availability, and in catfish, the filter changes with training procedures. One might assume that many fishes can simultaneously have many different filters in their smell brain. Under different circumstances, different filters are activated — for instance, in the search for food, home, mate, or predator. All fishes studied so far also have taste. But taste appears to regulate food intake, the actual reflexes that take place during the act of feeding.

These brain-behavior criteria apply to fishes and man, and probably also to arthropods. When one stimulates the small antennae (smell) of the lobster with mussel juice, the animal will start searching in the immediate area, probing with antennae and feet, and displaying feeding motions when the stimulus is strong. When one stimulates the dactyl receptors on their feet (taste), they open and close the little claw and poke around with that foot. With stronger stimuli they respond with a few more feet, and eventually they show complete feeding behavior. It seems that taste stimulates localized reflexes, whereas smell puts the entire animal in the feeding mode. Other recent experiments showed that smell lesions did not affect a lobster's food manipulation behavior much, but taste lesions had specific effects on the stereotyped sequence of events that takes place when a lobster encounters a live mussel. When we add to these experiments the fact that crab sex pheromones (attractants) and host odors are perceived with smell and not with taste, it becomes possible to equate the lobster's chemoreceptor organs with those of vertebrates — as far as their biological function is concerned. Since similar — and in some cases even better — arguments can be made for insects, we may perhaps generalize and feel a little easier about speaking of the senses of smell and taste in bees, crabs, dogs, fishes, and man. In all cases, taste is used for reflex behavior, often associated with food intake, and smell creates plastic filters (through which the chemical environment is viewed) that stimulate and motivate the animal into various behavior patterns, such as home recognition, prey hunting, predator avoidance, and mate selection. To exaggerate the differences between smell and taste: taste acts — smell thinks.

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Vision Underwater

Squid (Doryteuthis plei). *(Photo by Jen and Des Bartlett, PR)*

by Joseph S. Levine

Vision in the marine environment is a difficult proposition for humans. If you have never opened your eyes underwater, imagine trying to see through a fog while wearing prescription sunglasses designed for a very nearsighted person. The severity of the fog and the color and density of the glasses would depend on the type of marine area you wanted to simulate. For example, the rather clear environment of a tropical coral reef would require a hazy summer day and glasses tinted light blue. A north-temperate coastal area could be simulated by a medium fog and dark green sunglasses. An estuary, however, would require the densest pea-soup fog and the darkest amber or reddish-brown glasses available. In shallow water, there would be more visual confusion. Waves and ripples moving across the water's surface cause variable refraction of sunlight that creates an endless succession of moving light and dark areas. As the observer descends into deeper water, the total amount of light decreases rapidly with increasing depth — even in clear water — and the light becomes more and more distinctly colored.

Dim light, fog, colored light — each of these situations places constraints on visual performance that are distinctly different from those normally encountered by terrestrial animals. The eyes of aquatic animals have shown remarkable evolutionary plasticity in adapting to the rigors of this underwater visual environment. Even within single families of fishes, one can find eyes that have changed their size, shape, retinal organization, and wavelength sensitivity so dramatically that from looking at the eyes alone one would never suspect the species were closely related. A cursory examination of these varied visual systems can therefore proceed with apparent flagrant disregard for evolutionary constraints, which are obvious in the visual system only at more subtle levels, but it must be conducted in tandem with a discussion of the features of the submarine environment that so drastically affect the passage of light.*

Optically Important Interfaces

Why would an eye designed to work in air become seriously farsighted (hyperopic) when submerged? Water is a denser medium than air — an apparently incidental (and obvious) observation that turns out

*This article will focus on adaptation of the peripheral sensory apparatus to environments characterized by light of different intensity and wavelength distribution. Stimulus processing at higher levels of the central nervous system provides selectivity and filtering mechanisms concerned with movement and shape as well as color and brightness, but these mechanisms are beyond the scope of this article.

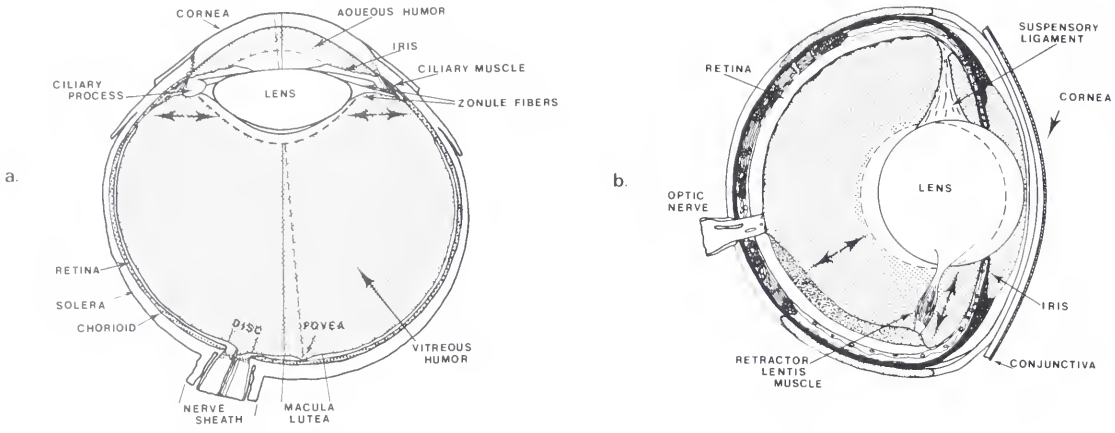


Figure 1. (a) Cross section of human eye. Note the lens-shaped cornea, the oval lens, and the ciliary muscles that change the shape of the lens for focusing. (From Walls, 1942). (b) Cross section of a typical fish eye. Note the round, solid lens that protrudes almost to the point of touching the cornea and is focused by moving back and forth with respect to the retina. (From Walls, 1942)

to have major consequences for the design of aquatic eyes. The density of the operating environment for any device that needs to bend light in order to focus it is critical because the amount of refraction that occurs at an interface depends on both the curvature of the boundary between the two media and the difference in their density-dependent *refractive indices*. The optically important interfaces in the vertebrate eye occur where the external medium — air for terrestrial animals, water for aquatic ones — abuts the cornea, and at the front and back edges of the lens where it meets the aqueous and vitreous humor, respectively (Figure 1). The difference in refractive index between air and the typical cornea and aqueous humor is substantial. In nonaquatic environments, a good deal of refraction (hence, light gathering and focusing) can be effected by a cornea that is properly curved to act as a lens. Very little additional refraction is actually necessary to form a clear image on the retina, so this task can be accomplished by an oval lens not much denser than the aqueous and vitreous humor in which it operates. Lenses in this density range are malleable, and are focused by contraction and relaxation of a muscular ring that surrounds the lens and can change its shape (Figure 1a).

In an aquatic situation, on the other hand, the refracting power of the cornea is severely diminished by the high density of the surrounding water. Even if an aquatic cornea was properly curved, it simply could not focus light the way it could in air. The lens must therefore accomplish substantially more refraction in aquatic eyes, both to gather light and to project it accurately onto the visual cells of the retina. Typical terrestrial lenses just cannot undergo the radical changes in shape necessary to make this compensation. Light rays are not brought into focus on the plane of the retina, and hyperopia results.* The majority of aquatic vertebrates — and those eagle-eyed invertebrates, the cephalopods (such as squid) — have solved this problem by developing round, crystalline lenses of high density that protrude through the pupillary opening. The highly curved shape of these essentially solid lenses cannot be changed to any great degree, and light is focused by changing the position of the lens with respect to the retina, through the action of a unique muscle and ligament combination (Figure 1b).

The ubiquitous underwater fog that degrades image quality over distance is caused by an optical phenomenon known as *scattering*. Scattering also gives rise to a situation where light impinges on objects underwater from all directions at once. A shaft of sunlight passing through clean air is virtually undetectable when viewed from the side. The gaseous air molecules offer little obstruction to visible light over short distances. Visible light rays passing through air travel in straight lines until they strike objects that either reflect or absorb them, and the light reflected from objects in one's visual field travels unobstructed until it reaches the observer's eyes. If, however, the path of the sunbeam (that is invisible when viewed from the side) is crossed by a cloud of dust or smoke, the beam instantly acquires visibility as the minute suspended particles interfere with the light rays, deflecting or scattering some of them sideways toward the eyes of the

*Certain amphibious vertebrates have exceptionally flexible lenses that can change shape to an unusual degree, permitting them to see well both in air and in water, but this ability is lacking in most other animals. Scuba divers circumvent the difficulty by taking along a small volume of air in their masks to maintain terrestrial corneal function underwater.

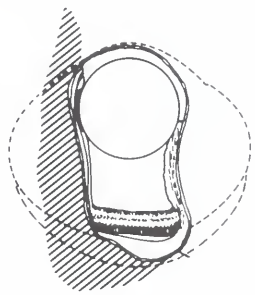
observer. Naturally-occurring bodies of water, no matter how chemically pure, are rarely as clean as air — they almost always carry a substantial load of fine silt and larger particulate material. As sunlight streams down through a water mass, these particles and even the water molecules themselves scatter light randomly in all directions, including directly back toward the point of origin (Figure 2). Light scattered horizontally is responsible for an even background radiance known as the *background spacelight*. It is against this backdrop that objects in the pelagic environment must be detected. Light scattered back toward the surface from below the level of the observer — and reflected off the bottom in shallow water — is responsible for the eerie glow from the depths characteristic of clear-water habitats. Scattering between objects and observers gives rise to the phenomenon known as *veiling brightness* which, along with the scattering of rays emanating from the object itself, causes a severe decrease in both the sharpness and contrast of the visual image with distance.

Since the light rays scattered out of the downwelling illumination are effectively subtracted from the total energy traveling downward, scattering is one cause of the dramatic drop in ambient light with increasing depth that is characteristic of all aquatic environments. Although light travels through the atmosphere for several thousand meters before it reaches the earth's surface, passage through 170 meters of even the clearest water lowers the intensity of sunlight sufficiently to make photosynthesis impossible and vision extremely difficult.

Increased Eye Size at Greater Depths

In fishes, the evolutionary response to diminished light at greater depths is dramatic at all levels of organization in the eye. The first noticeable change is an increase in eye size. Indeed, some twilight-active shallow-water species, and deep-sea fishes that live in eternal twilight, have eyes blown up to the point where there is barely enough room for them. In deeper-dwelling species, the pupillary opening and the lens have continued to expand out of all proportion to the rest of the eye, producing optical devices with very limited fields of view but with outstanding light-gathering ability (Figure 3a). In the abyssal depths, where practically the only light available is the dim, blue glow of bioluminescence,* these tubular eyes are found to point either forward or upward, depending, apparently, on the behavioral requirements of the species (Figure 3b).

*The emission of light from living organisms as the result of internal oxidative changes.



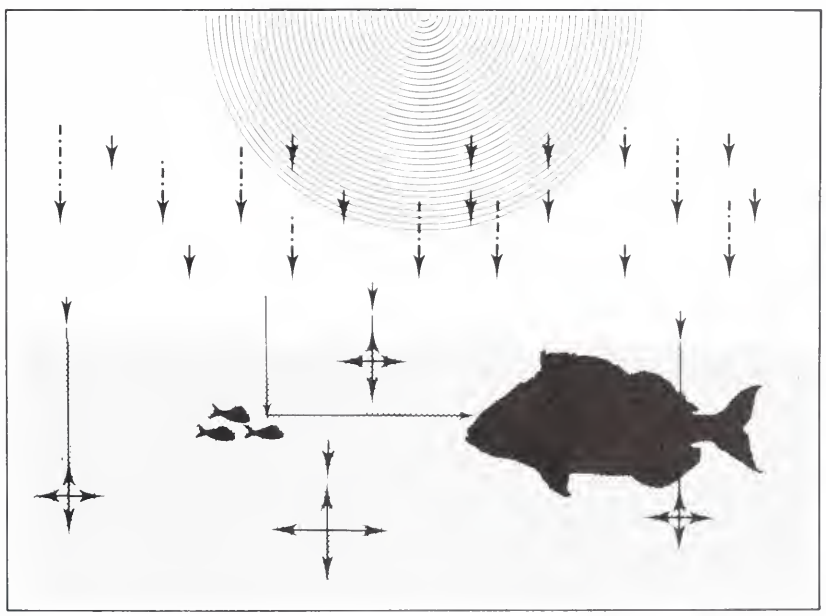


Figure 2. Light scattering in aquatic environments.

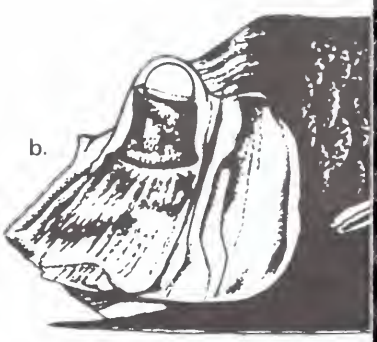


Figure 3. (a) Tubular eye of Argyropelecus, *a deep-sea fish. The effective aperture of this eye is equal to that of a much larger, normally shaped eye. The large, round lens, unobstructed by an iris, gathers light with great efficiency. (b) Typical tubular-eyed fish. (From Walls, 1942)*

The cellular components of the retina and their patterns of organization show similar expansions when they must function in limited light. In diurnal, shallow-water fishes, both the high-light receptors (cones) and the low-light receptors (rods) are small, tightly packed, and very numerous (Figure 4a). Paired cones and single cones are usually present, arranged in regular, geometrically uniform mosaic patterns (Figure 4b). The single rods are usually forced to a peripheral level in the light-adapted retinas of such species. Fishes that must use their eyes at greater depths (or during twilight periods in shallow water) have cone cells that are enormously enlarged compared to the high-light species, that is, fishes in areas of high-intensity light (Figure 4c).

What is the reason for this change in cone size? The physical correlate of light intensity is *photon flux density:* the number of photons (particles that compose light) that pass through a given area per unit time. As light intensity drops, the number of photons striking a cell of a given size per unit time will diminish. A finite number of photon absorptions must occur in a cone on a regular basis in order to cause it to produce a neural signal. It is believed (but not yet proved) that if the size of the receptor cell were larger, the cell's chances of catching sufficient photons at low flux densities (in dim light) would be greater. Along with the enlargement of individual cone cells, the cone mosaic itself expands, and its regularity falls by the wayside as single cones come and go, and triple cones — whose visual pigment contents and function are still unknown — intrude into the pattern unpredictably (Figure 4d). The wide spaces left between the cones are occupied by tightly packed, numerous rods which play a critical role in low-light vision. Individual rods require fewer photons to excite them than do individual cones, and rods are hooked up in neural networks that combine or *summate* signals from larger numbers of receptors. Summation allows a pooling of many small signals to form fewer large ones. The increased sensitivity afforded by this arrangement has its price; visual acuity (resolving power) is significantly lower in these eyes than in those of shallow-water, diurnal species.

Below certain levels of ambient illumination, however, there is simply not enough light for even enlarged cones to function, and they frequently disappear or become vestigial (Figure 4e). In a typical deep-sea species, cones are virtually nonexistent; the rods take over the retina completely. Figure 4f shows a species in which the rods have multiplied extensively and have become stacked into several layers. Since only a portion of the light that strikes a visual receptor is absorbed while passing through the cell, the existence of several layers of cells increases the light-catching potential of the retina substantially.

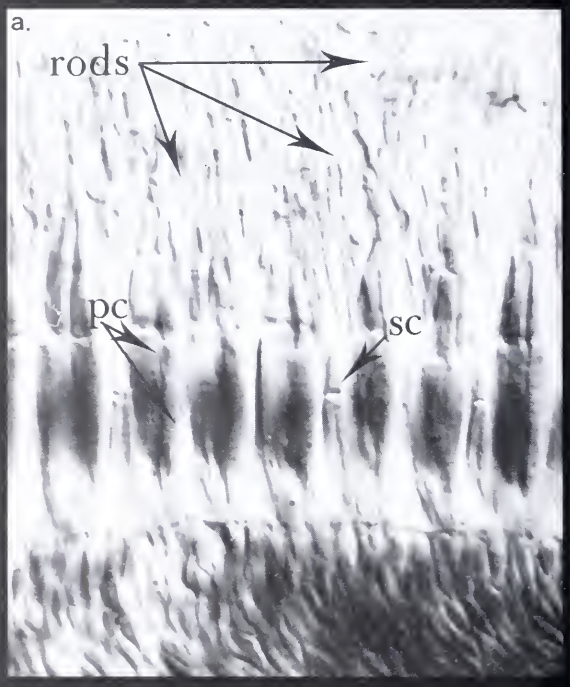
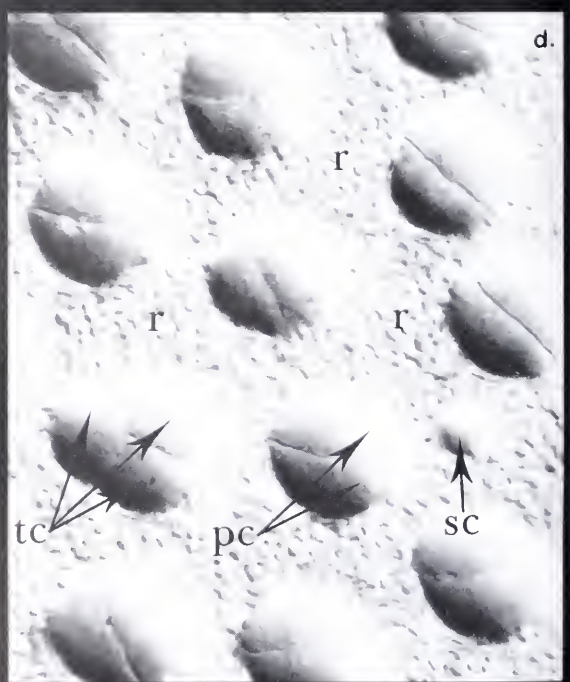
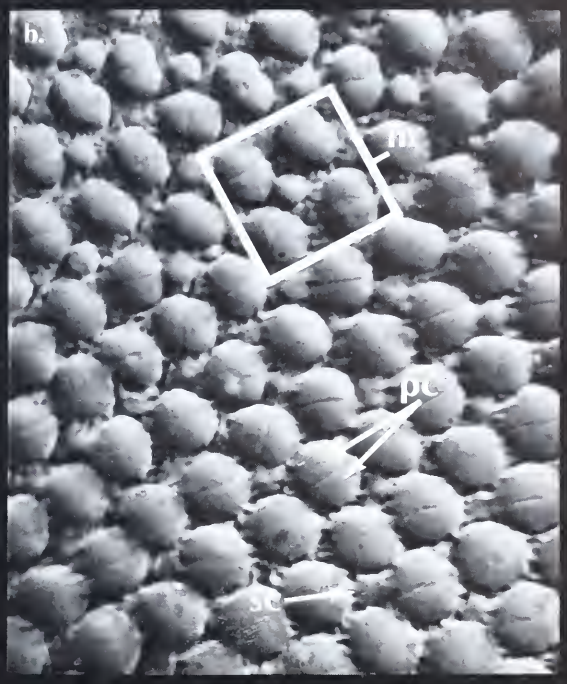


Figure 4. (a) Section of mackerel (Scomber scombrus) retina showing slender, tightly packed paired cones (pc), single cones (sc), and rods (r).

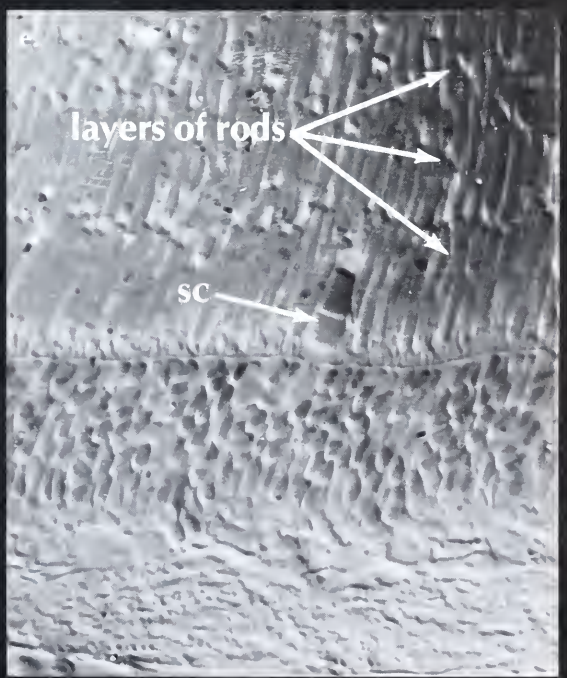


(d) Cross section of cusk retina showing decreased regularity in spacing and arrangement of cones, which include one triple and one single cone. In cusk, the numerous rods completely fill the space between the cones.



*(b) Cross section of the wolffish (*Anarhichas lupus*) retina, showing regular, repeating mosaic unit (m) of one single cone and four paired cones, with a few rods visible in the spaces between cones.*

*(c) Retinal section of cusk (*Brosme brosme*) at same magnification as (a), showing greatly enlarged, widely spaced cones, and numerous long rods.*



(e) Retinal section from the still deeper-dwelling fawn cusk eel, Lepophidium cervinum *(same magnification), showing a single, small cone and a retina overwhelmingly dominated by rods.*

(f) The cusk eel retina (at lower magnification) showing the tiered arrangement of rods.

Histological preparations courtesy of Barbara-Ann Collins.

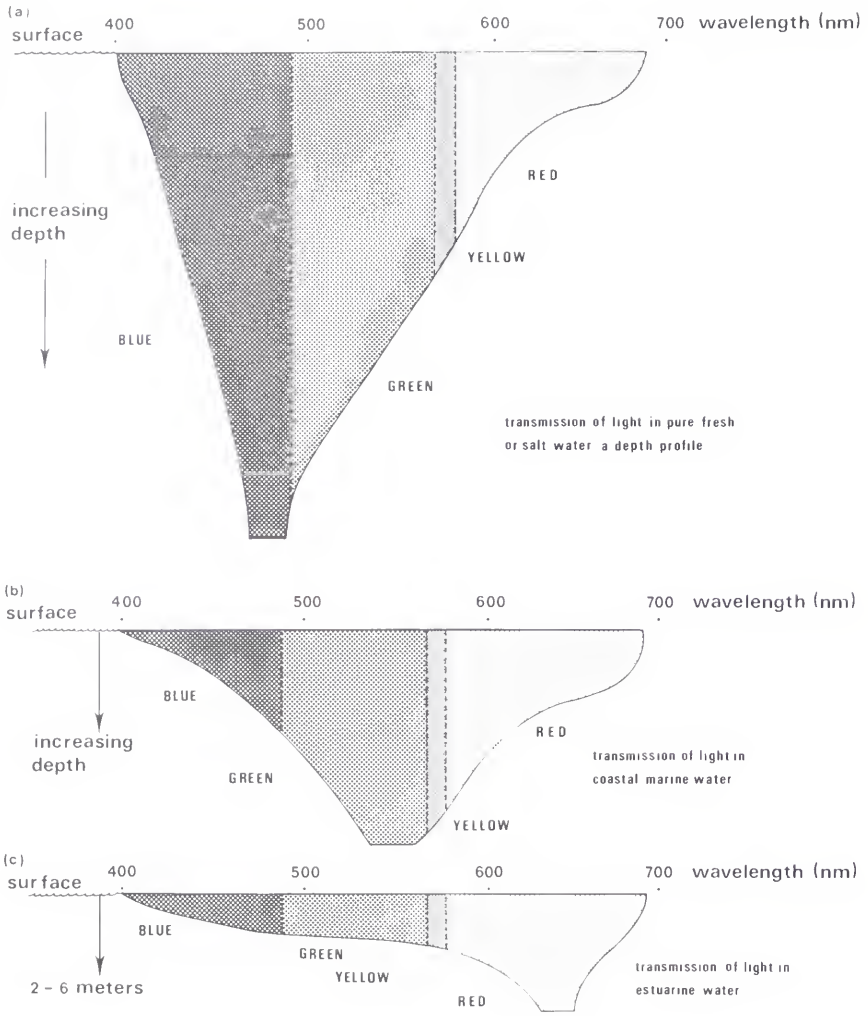


Figure 5. Transmission of light of various wavelengths through natural bodies of water: (a) clear oceanic, (b) coastal marine, and (c) estuarine.

The Coastal Environment

Just as the visual receptor cells' size and organization must be adapted to the intensity of ambient illumination, so also must their spectral sensitivities be adapted to suit the color of the photic environment which, as noted earlier, varies with depth, as well as from one habitat to another. Water molecules, and the assorted dissolved substances they often carry, differentially absorb various wavelengths. Pure oceanic seawater strongly absorbs ultraviolet, red, and infrared wavelengths while transmitting maximally in the blue region of the spectrum (light of wavelength 475-485 nanometers*). (We simulated this effect earlier using light-blue sunglasses.) Coastal marine waters usually contain higher quantities of dissolved organic compounds and may carry a large amount of phytoplankton depending on the season. These substances absorb shortwave light very strongly and would exhibit a yellow cast if isolated, but superimposed on the basic blue character of seawater, they impart a medium green color to such environments. The wavelength of maximum transmission in coastal waters is usually at about 550 nanometers. Estuarine areas, which often contain substantial concentrations of several larger organic molecules released from decomposing vegetation, transmit very little light at wavelengths below 600 nanometers. This type of water usually is reddish brown or dark amber (Figure 5).

In habitats where the light is both dim and distinctly colored, the relationship between visual cell spectral sensitivity and photic environment is straightforward. All visual cells owe their light sensitivity to photolabile* chemicals called *visual*

* A nanometer is one billionth of a meter.

* Capable of being changed by light.

pigments, which are capable of interacting with light of certain wavelengths. When a visual pigment molecule absorbs light, it undergoes a series of structural alterations that — in a manner still not completely understood — trigger electrochemical changes in the photoreceptors that contain them. Visual pigments are capable of absorbing light of most visible wavelengths to some degree, but the *absorption spectra* that characterize the probability of pigment interactions with light of various wavelengths exhibit pronounced *absorption maxima* which differ from one visual pigment to another (Figure 6). The steep slope of these curves on either side of the maximum indicates that these pigments are far more efficient in detecting light near those maxima than elsewhere in the spectrum. For this reason, any mismatch between visual pigment absorption maxima and the color of ambient illumination in light-limited environments would be ill-adaptive. Another demonstration with sunglasses can make this point clearer. This time, imagine that you are in a dimly lit theater, and the color of your sunglasses represents the spectral sensitivity of your sole visual pigment. If the stage is bathed in blue light and you don a pair of blue sunglasses, you will be able to see reasonably well; your sensitivity is matched to the available illumination. If, however, you were to choose a pair of green or rose-colored glasses, your visual sensitivity would be severely diminished, and everything would be much darker. The same would be true of matched and mismatched visual pigments in deep-sea fishes. Many studies have shown that the rod visual pigments of marine species cluster tightly around the transmission maximum of whatever type of seawater the organisms inhabit.

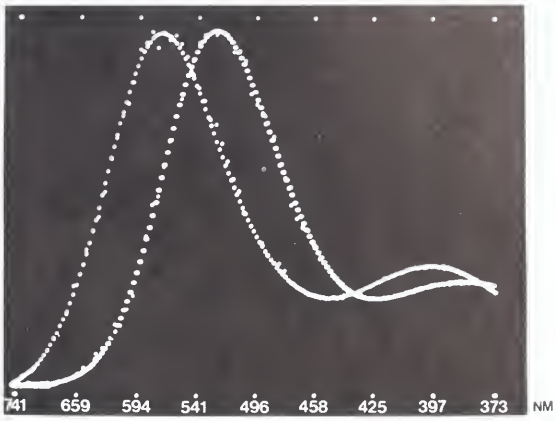


Figure 6. Computer-generated curves representing the absorption spectra of two visual pigments with different absorption maxima, graphed as optical density across the spectrum. The height of the curve at any given point in the spectrum indicates the relative probability that light of a particular wavelength will be absorbed.

Vision Used for Different Purposes

If you are to wear your sunglasses in full sunlight, the color you choose for the lenses is a matter of preference and the nature of the tasks you need to perform while wearing them. Perhaps blue glasses would suit you best during a nature walk when looking for yellow wild flowers, whereas red might help you pick out pizzas with the best tomato sauce. In fact, since it is inconvenient to change one's glasses for every occasion, there is no reason why you couldn't choose one color for each eye. This arrangement, which would enable you to perform certain visual discrimination tasks more accurately than would be possible with glasses of either color alone, is analogous to the situation created by multi-pigment visual systems.

Although a visual system based on a single visual pigment has advantages in spectrally restricted, low-light environments, such a system can be easily confused by stimuli of different wavelengths. In other words, an animal with a single-pigment visual system is colorblind. This organism sees an image of the world much like that produced on a black and white television set, composed only of black, white, and shades of gray. Dark blue objects are indistinguishable from dark gray or red ones, and white could be confused with bright yellow. In order to tell objects apart on the basis of the wavelengths they reflect, an organism needs a minimum of two mechanisms with different spectral sensitivities. It is by comparing the responses of these mechanisms that animals acquire color vision.

Current research indicates that animal species (including man) that inhabit brightly lit environments have usually done precisely this by evolving two or more classes of cone cells, each of which contains a different visual pigment, and by developing neural networks to compare the signals from these different classes. Many fishes have color vision that seems to be as highly developed as our own, but the specific demands of their environments often dictate ranges of sensitivities quite different from ours. Variations are to be expected in the cone pigments of fishes exposed to light of high intensity, since the light encountered even near the water surface is highly colored. Also, different species may use their eyes for different visual tasks, trading off with their other senses in innumerable ways. Some fishes use vision to hunt for food, but use other senses (for example, they produce loud noises) to find mates; whereas others use chemoreception to find food but use vision to spot prospective mates.

Work done at Princeton by John Endler has shown the importance of body color patterns in predatory-prey and courtship behaviors among fishes that depend on vision in these activities. Strikingly colored guppy males are seen easily and

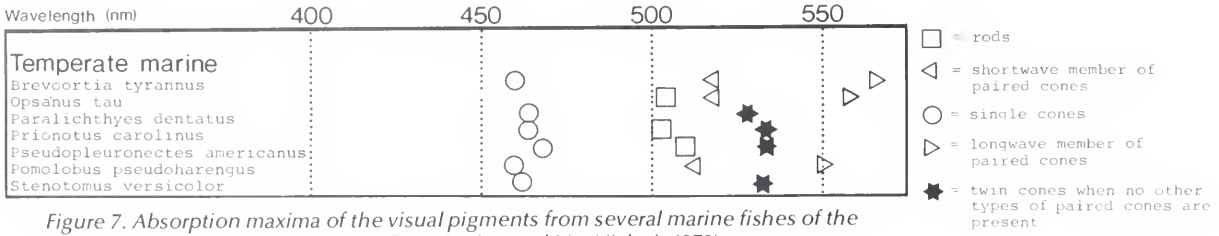


Figure 7. Absorption maxima of the visual pigments from several marine fishes of the Woods Hole, Massachusetts, area. (From Levine and MacNichol, 1979)

preferred as mates by guppy females, but they can also be quickly singled out by visually hunting predators. If guppy visual systems differed substantially from those of their predators (and it appears that they might), it would be possible for guppies to evolve body colors that are conspicuous to other guppies, but inconspicuous to predators. It is important to realize that prey vision, predator vision, and prey body color are not static, but rather are all subject to evolutionary pressure that ties them together into a close, co-evolving network. A scientist examining any part of the network must be aware that the existence of this dynamic, behaviorally dependent relationship makes it risky to make simple assumptions regarding the effect of water color alone on visual system evolution.

Data on visual pigments and visual behaviors in freshwater fishes are scarce, but information on vision in marine fishes is scarcer still. In most cases, observations on the visually related behaviors of marine species are practically nonexistent. The difficulty in determining where, when, and for what purposes fishes actually use their eyes is particularly severe in the case of temperate marine faunas. Whereas tropical biologists can delight in species with super-specialized feeding habits and restricted depth ranges, those working with temperate fishes must be content with species that eat virtually anything that moves and range from just below the tide line to more than 180 meters.

Nonetheless, it is clear that the retinas developed by inshore, temperate marine fishes are of two types, differentiated by the nature of the paired cones (Figure 7). In some species, the paired cones are *twins* that contain the same visual pigment. The absorption maxima of the pigments found in such twin cones closely match the predominantly green light of the coastal waters. Pigments matched to the background light in this manner would help in maximizing the visibility of dark objects silhouetted against either the downwelling light or the background spacelight. Theoretically, the twin cones could also make the retina more sensitive (than could an array of single cones) to wavelengths that predominate in the environment, but this hypothesis awaits laboratory confirmation. Other species that share the habitat have paired cones with different visual pigments whose absorption maxima neatly straddle those of neighboring species' twin cones. These so-called offset pigments would help to increase the visibility of highly reflective objects against the background when the observer is in shallow water. All of these fishes have visual pigments that are strikingly different from those of most freshwater species.

It is clear that marine vertebrates have visual systems that cover the full range of complexity from simple, all-rod, one-pigment systems to highly developed rod and cone retinas with both the visual pigments and the neurological network for well-developed color vision. When it comes to understanding the selection pressure responsible for the evolution of these systems, however, we have advanced but little from the time when Goethe wrote with curiously inverted logic that "color is an elementary phenomenon of nature adapted to the sense of vision." We now firmly believe that the exact opposite is true, and several more generations of researchers will find much to occupy their time in attempting to understand the complexity of visual systems.

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Acknowledgments

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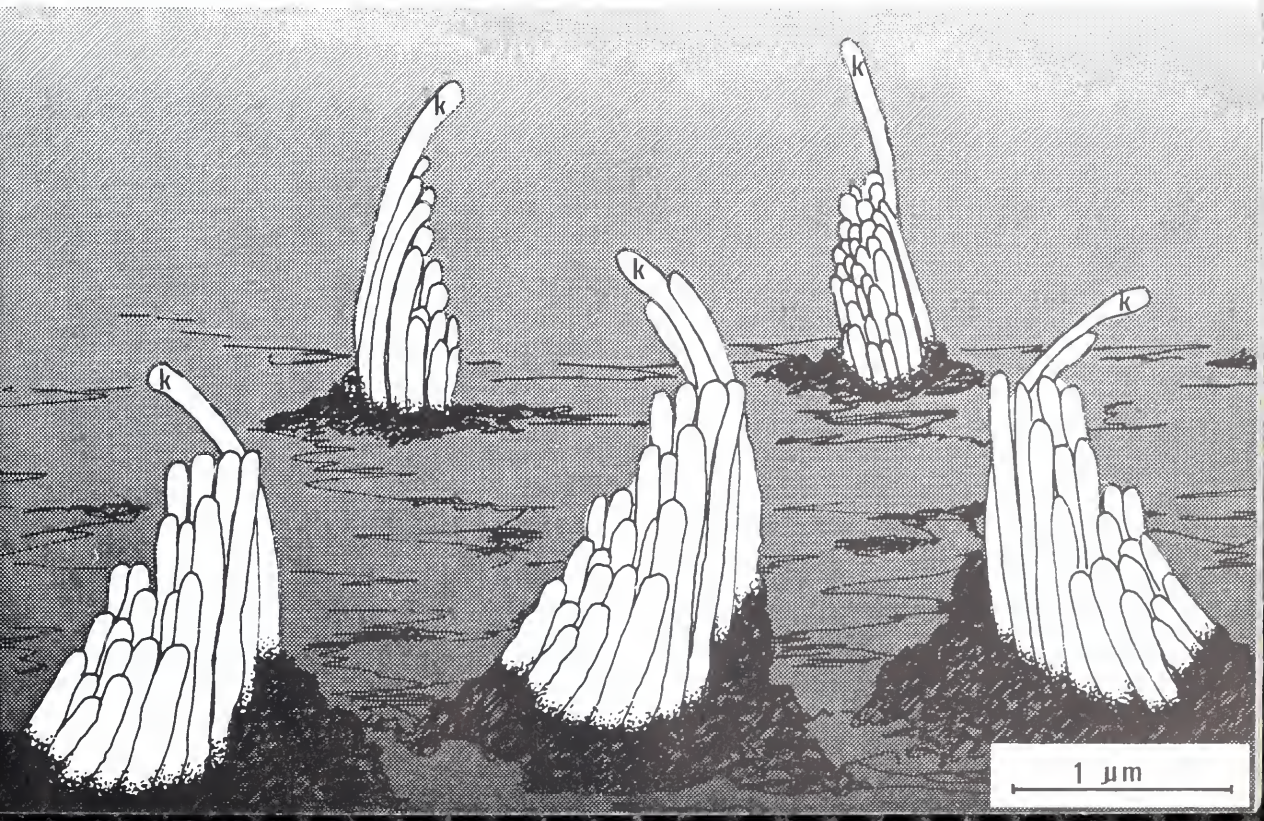
Fish Hearing

by J. H. S. Blaxter

When we dive we perceive the underwater environment as being rather silent. Our ears are not tuned to the physical nature of underwater sound. Actually, the sea can be a rather noisy place. Near the surface, background noise by surface wave action may greatly mask other noises, especially in bad weather. Fishes generate internal noise by passing through the water and by the contractions of their own bodies during swimming. Adjacent fishes — schooling mates or predators — also create a variety of mechanical stimuli by swimming movements.

Artist's impression of the surface of the macula as seen by a scanning electron microscope. The otolith has been removed and the sensory hairs can be seen projecting above the macular surface. K = kinocilium.



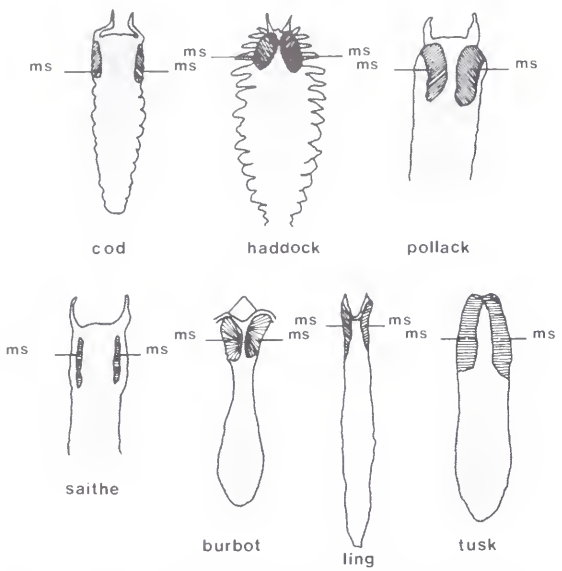


Figure 1. Swimbladder muscles (ms) implicated in sound production in several gadoid (cod-like) fish species. The swimbladders are shown removed from the fish. (After Freytag)

Some species produce sounds (often of sexual significance) by drumming muscles (Figure 1), which cause the swimbladder to pulsate. In general, fishes must produce sounds as a result of feeding, which may be attractive if prey are involved, or repulsive if caused by a predator. Some invertebrate prey species, especially crustacea, may produce stridulatory sounds (like running a finger along the teeth of a comb) or attract fish predators by their swimming movements.

Most of these noises will be of low frequency — in the range of a few Hertz (Hz) to hundreds of Hz. Higher frequencies may be created by the echolocation calls of marine mammals (see page 69) or perhaps by diving birds. The ranges of frequency are:

1 Hz — hydrostatic pressure changes, probably only perceived by the acoustic system in clupeoids (such as herring)
3-35 Hz — tail beats
50-400 Hz — sound production
several kilohertz (kHz) — echolocation of marine mammals

Many species cannot respond to sounds above a few hundred Hz. However, the ostariophysine and clupeoid fishes (which will be discussed in more detail later) have high-frequency responses. The ostariophysi in particular are unlikely to be preyed on by marine mammals. The explanation may lie in the enhanced ability of these fishes to respond to transient noises, and furthermore, to respond very quickly to the onset of a stimulus. Many fishes have Mauthner cells in the spinal cord — giant nerve fibers closely linked to the auditory nerve — which cause a very rapid body contraction leading to a fright response. It may be vital for the survival of prey species to react quickly to transient noise, perhaps by producing a tail flip when a predator approaches suddenly.

Another hazard to fishes is the predator, man. A considerable amount of research on fish hearing has been justified by the need to know whether fishes can respond to propeller beats from a fishing vessel or to the approach of a net, and whether they can make directional avoidance responses. It seems likely that their ability to perceive direction is better than that which might have been predicted by physiological evidence. Fishes must overcome the problem of perceiving direction when a pulsating (apparently nondirectional) source within the fish, the swimbladder, is the main source of stimulation. Recent experiments show that fishes with swimbladders do have directional perception. Training experiments also have been conducted to lead fishes from one sound source (where food is provided) to another, or to hold them without retaining nets around a food source (an acoustic signal was used as a conditioning stimulus). Attracting untrained fishes to feeding sounds of their own species (played through an underwater loudspeaker) may also prove a useful method of aggregating them prior to capture. Information on frequency response, threshold, and directional perception is essential for manipulating fishes in this way.

Sound Underwater

Sound has much to recommend it as a form of sensory stimulus in the underwater environment (see *Oceanus*, Vol. 20, No. 2). It is transmitted at high speed through turbid water and in darkness, where visual stimulation is impossible. Information can be encoded in terms of frequency, amplitude, and pulse length. Unlike a chemical stimulus, sound does not persist, which may or may not be an advantage to the species concerned. The propagation speed of sound in water is approximately 4.5 times greater than in air — 1,500 meters per second — and very little incident energy passes across the water-air interface.

Sound sources provide two types of stimulation — a sinusoidal change in pressure, which can be measured by a hydrophone; and a back-and-forth motion of water (expressed as particle displacement or particle velocity), which is more difficult to measure, requiring velocity meters in three planes. Pressure and particle motion are related to each other and to the distance of the sound source. Particle motion can give information

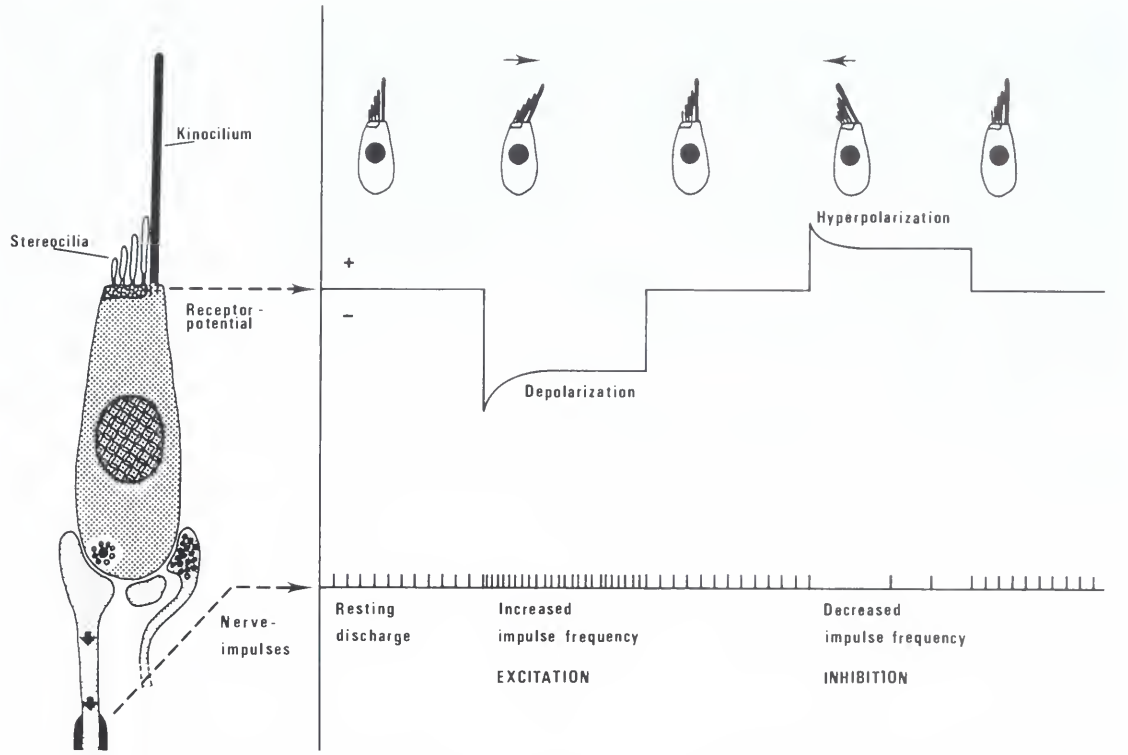


Figure 2. A neuromast sense cell, showing the two types of sensory hairs at the tip of the cell and the nerves at the base. The directional properties depend on whether the kinocilium is bent away from or toward the stereocilia by the stimulus (as shown by the arrows). In the first case, the cell becomes depolarized with respect to the surroundings, causing it to fire (excitation). In the second case, the cell becomes hyperpolarized with an inhibitory effect. (After Flock)

about the direction of the sound source, but pressure cannot. Far from the source, sound pressure and particle motion are related by a simple ratio. Near the source (within the so-called near field), sound pressure falls off as $1/r$ where r is the distance from the source, whereas particle motion falls off as $1/r^2$ for a pulsating source (such as a fish swimbladder) and as $1/r^3$ for a vibrating source (such as a fish tail). In the far field, both sound pressure and particle motion fall off as $1/r$. Within the near field, particle motion predominates and displacement receptors within the organism are especially important. In the far field, pressure receptors are more important. Usually the change from near to far field is taken as a distance of about $\lambda/6$ from the source, where λ is the wavelength of the sound.

The Receptors

Particle displacement is sensed by mechanoreceptors. The mechanoreceptors of fishes are located in the acousticolateralis system which comprises the inner ear and the lateral line. In both the ear (labyrinth) and the lateral line, the basic receptor is the neuromast organ. This consists of a group of sensory cells, each with a bundle of ciliary hairs embedded in a gelatinous cupula (Figure 2). Most hairs are rod-like structures called stereocilia, and each cell has one longer kinocilium (see illustration at beginning of article). Electron microscope studies show that the kinocilium has a core of nine filaments. This is also characteristic of motile cilia and other sensory cells in the eye and nose. The neuromasts have directional properties (Figure 2). If the kinocilium is bent away from the stereocilia, the cell becomes depolarized and fires; if it is bent toward the stereocilia, the cell becomes hyperpolarized with an inhibitory effect.

Groups of neuromast cells are found aggregated either into the neuromast organs in the lateral line, or into sensory areas in the labyrinth. Those in the lower part of the labyrinth are called maculae (Figures 3 and 4). The basic sensory unit is the same in both areas, but the sense organ as a whole is adapted to respond to different types of mechanical stimulation — to sound, linear and angular acceleration, gravity, or localized water movement outside the body. Some organs may respond to more than one of these forms of stimuli.

The maculae have an adaptation of the

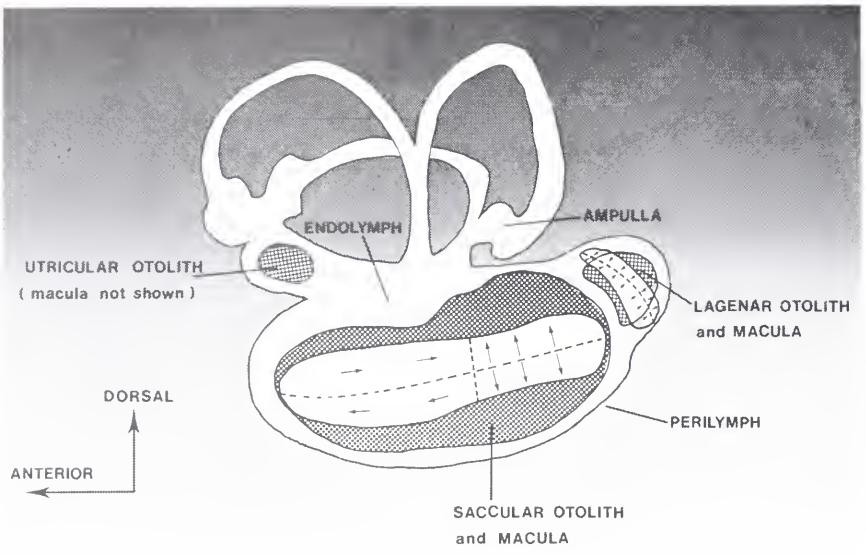
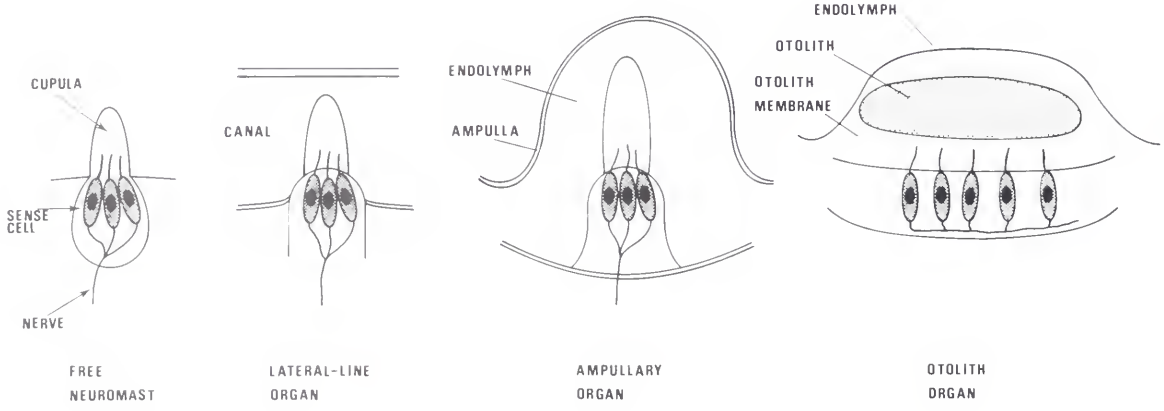


Figure 3. A generalized fish labyrinth. The shaded areas show the limits of the otoliths. The macula is mainly below the otolith. The arrows within the limits of the macular surface give an idea of the variation in orientation of the kinocilium in relation to the stereocilia. The utricular macula, which is important for hearing in clupeoid fishes, is not shown, nor are the sensory areas and their hair cell patterns in the ampullae. (After Enger)

Figure 4. The free neuromast organ is the basis for more elaborate structures in other parts of the sensory system.



cupula (see Figure 4) which has become specialized by the formation of an otolith membrane. Part of the cupula's otolith membrane is calcified, forming the otolith. In a sound field, at least at low frequencies and near the source, the fish is likely to respond as one unit to particle motion, because it is small compared with the sound wavelength and has a rigid backbone. The otoliths, which are more dense than the rest of the fish, will have an inertia and tend to lag behind the organism's movements. This causes the hairs of the macular sense cells to bend. Recent work, in which the otolith was removed, shows that the sensory hairs of the neuromasts have different patterns of orientation in different parts of the macula (Figure 3). A fish can probably detect the direction of a sound source depending on which part of the macula is most, or least, stimulated.

Along the lateral line, a different mechanism may be at work. There is a differential motion between the fish and the particles in the water surrounding the fish. This motion varies along the length of the organism depending on the distance from the sound source. Thus, with an elaborate series of canals in different orientations, each with characteristic axes of sensitivity to particle motion, the fish could tell where the sound came from.

Pressure Perception and the Swimbladder

Sound pressure falls off more slowly with sound source distance than does particle motion. Although sound pressure is the dominant stimulus at a distance from the fish (in the far field), the organism has no obvious sensory cells responding to sound pressure. Many species of teleost,

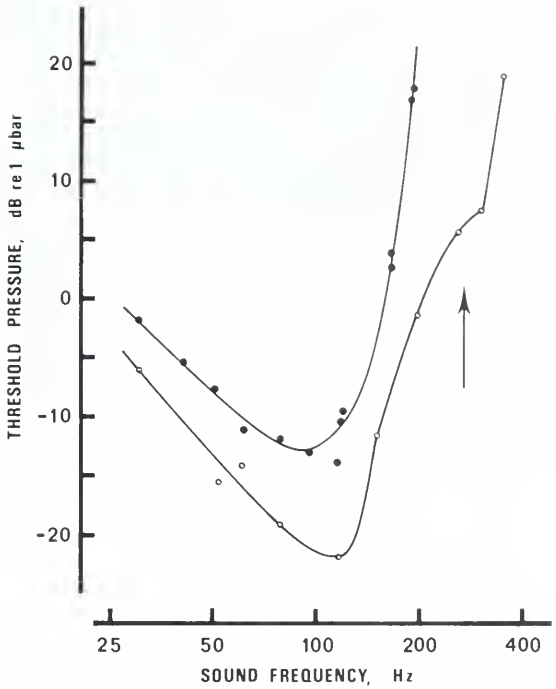


Figure 5. An audiogram of the dab, a fish without a swimbladder, with (○) and without (●) a small balloon by the head. The arrow shows the resonance frequency of the balloon. The threshold is given as sound pressure in decibels related to a reference level of 1 μ bar. (After Chapman and Sand)

however, have a swimbladder that responds to sound pressure by pulsating in sympathy with the passing compressions and rarefactions. The sound pressure will then be re-radiated as displacements, creating a secondary near field within the fish that can stimulate the displacement receptors.

Studies have shown that fishes with swimbladders have better hearing (in both frequency range and sensitivity) than fishes without. If the swimbladder is deflated, hearing is impaired. A neat experiment was performed on the dab, a flatfish without a swimbladder, which showed greatly improved hearing when a small balloon was placed near its head (Figure 5).

Specialization

In some fish families, such as the squirrelfish, the swimbladder and ear are very close. The wall of the skull may be thin where the two structures nearly meet. Two other groups of fishes have more elaborate specializations of the auditory apparatus linked with sound pressure perception — the ostariophysine and the clupeoid fishes.

1. The Ostariophysi, such as carp and catfish. These are characterized by the presence of Weberian ossicles — a linkage of three small bones

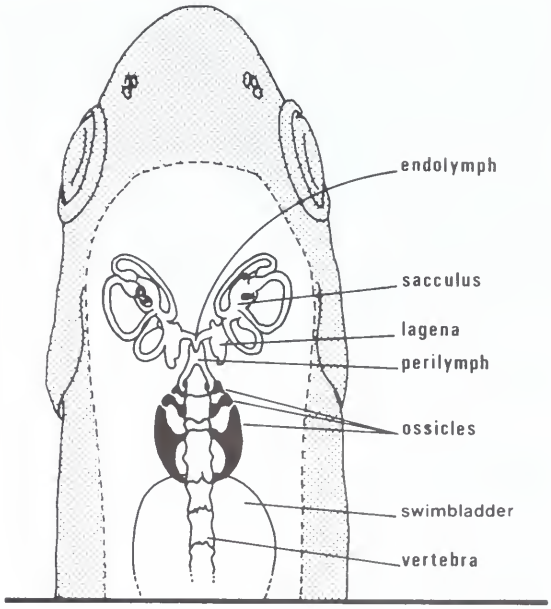


Figure 6. The Weberian ossicles in a species such as the goldfish (view from above), showing how the ossicles couple the swimbladder to the ear.

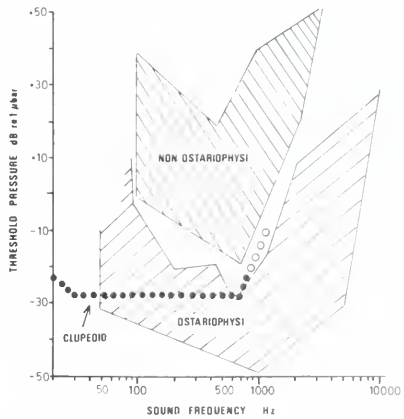


Figure 7. Audiogram "envelope" for different species of Ostariophysi and non-Ostariophysi and for a clupeoid, obtained by a variety of techniques. (After Popper and Fay; clupeoid audiogram by permission of J. A. B. Gray)

(evolved from vertebrae) connecting the swimbladder to the labyrinth (Figure 6). Swimbladder pulsations are thus transmitted to the hearing organs without weakening. The advantage of this can be seen by comparing the audiograms of ostariophysine and non-ostariophysine fishes. Both frequency range and sensitivity seem to be greatly enhanced by the Weberian ossicles (Figure 7). Some fishes without Weberian ossicles, however, also have very good auditory performances.

2. The Clupeoidea, including herring. This

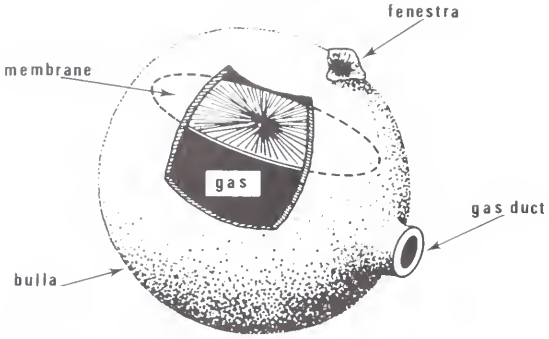


Figure 8. Clupeoid bulla, lateral-posterior view.

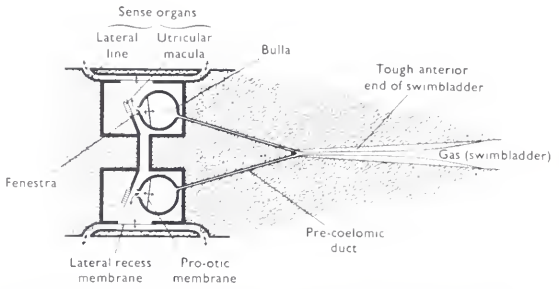


Figure 9. The clupeoid swimbladder-bulla-lateral line system. Arrows show movements of membrane and fluid in response to sound pressure changes. (From Denton and Blaxter, Journal of the Marine Biological Association, *Cambridge University Press, 1976)*

Figure 10. The head lateral-line system of the herring, drawn after an injection procedure (LRM = lateral recess membrane, N = neuromast organ). The herring and other clupeoids have no lateral line on the trunk.

group is characterized by the presence of a pro-otic bulla, a gas-containing sphere evolved from the bones of the otic (ear) capsule and situated directly in front of the labyrinth (Figure 8). The bulla is divided by an elastic membrane into an upper part filled with fluid (perilymph) and a lower part filled with gas. The perilymph is continuous with perilymph outside the labyrinth through a fenestra or window. The gas in the bulla is connected to the gas of the swimbladder via very fine ducts, only 4 micrometers * in radius. The bulla membrane vibrates in response to sound pressures, forcing perilymph in and out of the fenestra. The perilymph shears across the underside of the utricular macula (Figure 9), stimulating the hair cells above. Another membrane, the lateral recess membrane, is present in the lateral wall of the skull close to the bullae. The lateral recess membrane also vibrates in sympathy with the bulla membrane. It lies at the inner side of a cavity, the lateral recess, which is a central region from which all the head lateral-line canals diverge (Figure 10). The clupeoids thus have a unique coupling between the ear and the lateral line — movements of the bulla membrane stimulate both the utricular macula and the lateral line.

It should not be thought that sound is conducted along the fine gas ducts from the swimbladder to the bulla. The ducts represent a unique adaptation system that prevents the bulla membrane from bursting during a dive and keeps it in a flat resting state where it will be most sensitive (Figure 11). The bulla membrane is elastic; if the fish dives, the membrane bows in, but takes up much of the pressure. The swimbladder is, however, compliant to pressure, and a pressure difference is set up between the bulla and swimbladder, causing gas to flow along the gas duct into the bulla, restoring the membrane to its flat state. The time constant for this process is 15 to 30 seconds. If a fish moves up, the reverse occurs, and gas flows from the bulla into the swimbladder. In the herring, the anterior end of the swimbladder is especially thick-walled and noncompliant. Gas collects there (by the entrance to the gas duct) preferentially during a dive. The menhaden, a clupeoid with a short, deep body, has a swimbladder that is at a steep angle, with the anterior end much higher than the posterior end. This also helps to retain gas at the anterior end when pressure increases.

The hearing ability of clupeoids is enhanced by the presence of the bulla. The clupeoids also have the equipment to compare, within the head lateral-line system, outside particle motion and sound pressure (Figure 12). If the neuromasts can compare particle motion and sound pressure, they should enable the fish to determine the range of the source within the near field, where the two parameters are falling off at different rates.

Summary

Fish hearing in the near field is probably a function of both labyrinth and lateral line. In the far field, it is not clear whether particle motion can stimulate any of the sense organs. A swimbladder that transduces sound pressure into a localized secondary near field is probably essential. The swimbladder of teleosts

*A micrometer is one thousandth of a millimeter.

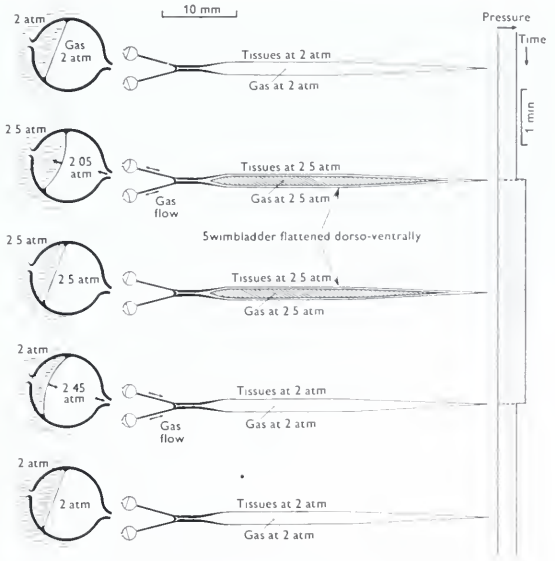


Figure 11. The mechanism for adaptation to hydrostatic pressure changes in clupeoids. A fish at 2 atmospheres (10-meter depth) experiences a quick pressure increase of 0.5 atmospheres for about 4 minutes before returning to its original depth. The time scale is shown on the right; arrows show the movement of gas between the swimbladder and the bullae. Note how the direction of the gas flow changes depending on whether the fish is compressed or decompressed. (From Denton and Blaxter, Journal of the Marine Biological Association, *Cambridge University Press, 1976)*

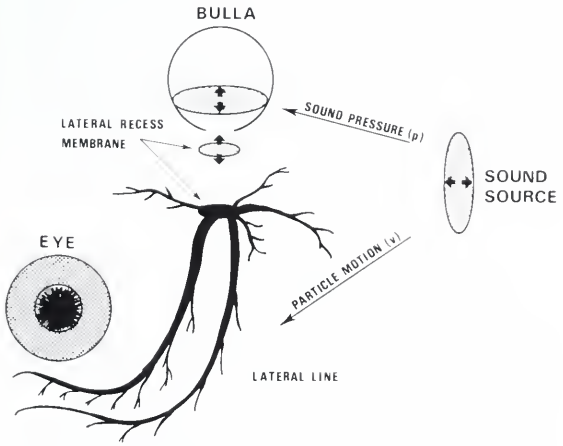


Figure 12. How the clupeoid lateral line could be stimulated by both sound pressure (p) via the bulla and particle motion (v) directly through the water. Since these are attenuated differently with distance in the near field, a comparison of p/v could enable the fish to detect the range of the source.

has evolved along several lines — from the most highly coupled system with Weberian ossicles, to others where anterior projections of the swimbladder are closely apposed to the ear. The clupeoids' problem is neatly solved by a gas-filled structure *within* the head, and as a bonus, it is linked to the head lateral line. The mechanoreceptors, although based on a standard unit, the neuromast, have evolved along different lines, so as to respond preferentially to angular or linear acceleration, to gravitation (posture) toward displacements caused by the passing of a sound wave, and to localized water currents. One must admire the presumed ability of fishes to filter out the noise created by their own swimming, to form highly coordinated schools with acoustic signaling, to avoid predators, and to be attracted to sound sources of beneficial origin. At present we do not know the extent to which fishes use sounds to avoid being caught by fishermen, nor the extent to which they use hearing to avoid nets.

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Equilibrium and Orientation

by Bernd-Ulrich Budelmann

Cephalopods, such as the pearly nautilus, octopus, cuttlefish, and squid, have long attracted the interest of scientists and laymen. Their capacity to change color within milliseconds, and their exceptional eye development — rivaling vertebrate sophistication — are well known. In addition, their highly developed central nervous system has a brain-to-body weight ratio exceeding that of most fishes and reptiles. Their learning capacities approach or even exceed those of many birds and even mammals. During the course of evolution, cephalopods developed an equilibrium receptor system whose structure, with some differences in organization, comes remarkably close to its vertebrate counterpart, the vestibular system.

Why did the invertebrate cephalopods evolve such a sophisticated system, one that is fundamentally different from that of all their close mollusk relatives? in 1972, the English zoologist A. Packard described the many parallels that exist in the organ systems of cephalopods and fishes. He argued convincingly that much about the evolution of cephalopods can be understood as soon as one realizes that these animals have always been competing with fishes.

As the first free-swimming animals of any considerable size — appearing in the late Cambrian (approximately 500 million years ago) — the cephalopods have had an unrivaled freedom to maneuver in the marine habitat. But this situation began to change in the late Paleozoic and early Mesozoic periods (160 to 230 million years ago) when the bony fishes spread into the seas. Since then, cephalopods and fishes have influenced each other in the struggle for life. The fishes produced the higher cephalopods, as Packard said. The great likeness of many of their organ systems probably has come about not merely as a response to similar physical demands of their environment, but also because of competition between the two groups. In this article, the remarkable sophistication and complexity of the equilibrium organs of these invertebrates will be discussed.

Sense of Equilibrium

Whether an organism is standing, walking, jumping, swimming, flying, or burrowing, the sense of equilibrium provides it with information regarding its attitude in the three dimensions of space. This information — combined with data from visual, tactile, and proprioceptive receptors (the latter measure the position of limbs and internal organs) — enables an organism to control its motor activities relative to gravity, thus controlling its orientation and behavior. Whereas other stimuli, such as odor, taste, light, and sound, may change or even be absent during periods of time, the gravitational field has a unique feature: during the life span of an organism, it is constant in magnitude and direction. It was thus natural that it be used as a reference system.

Nearly all aquatic and terrestrial animals (at least those which use locomotion) have evolved specialized sensing devices that use gravity as a reference system to detect changes in motion and position. These are the equilibrium receptor organs. In invertebrates, they are known as statocysts, fluid-filled vesicles that have calcareous particles, called statoliths, suspended within them. In vertebrates, they are known as vestibular end organs or vestibular apparatuses.*

The functions of these organs differ among animals depending on their life style and habitat. In the marine environment, the slow-moving mussels and snails require little orientational information; they may only need to know their position and movement relative to gravity (which in terms of physics is expressed as linear acceleration). Thus, their statocysts are only gravity receptor organs. In contrast, to maintain their well-balanced equilibrium, swift-moving animals may need to know not only direction of gravity but also angular

*In humans, the equilibrium system consists of a vestibular apparatus — a sac within a body channel — located in the inner ear. Hair cells act as mechanoreceptors which detect motion and position.

in Cephalopods

Cuttlefish. (Photo by Russ Kinne, PR)

acceleration, which results from any changes in motion or position involving rotation. Thus, they have developed two systems within the equilibrium receptor organs: one to detect gravity and another to detect angular acceleration. This occurs, for instance, in insects, the decapod crustacea (crabs, shrimp, and lobsters), the higher cephalopods (octopuses, cuttlefish, and squid), and fishes (Figure 1).

Although the two receptor systems have basic structural differences, they have one elementary physical concept in common: namely, that a mass, because of its inertia and loose connection to the organism, responds slower to changes in position than the organism itself. These movements by the mass are minute (in the range of about 0.01 to a few micrometers), and are measured by sensory cells lining the statocyst. These cells give information about magnitude and direction of movement.

Two examples bear out this principle. A person in a car experiences the results of sudden linear acceleration if his head is thrown back: the head (mass) through its loose connection (the neck) lags behind the forward motion of the body which is strapped to the seat. The magnitude and direction of the linear acceleration can be measured by the amount of displacement of the head relative to the body. Another example shows how angular acceleration works — when rotating a pan of water suddenly, the water will initially lag behind the rotation of the pan. Measuring the amount of lag between the water and pan indicates the amount of angular acceleration (sudden rotation). The head on

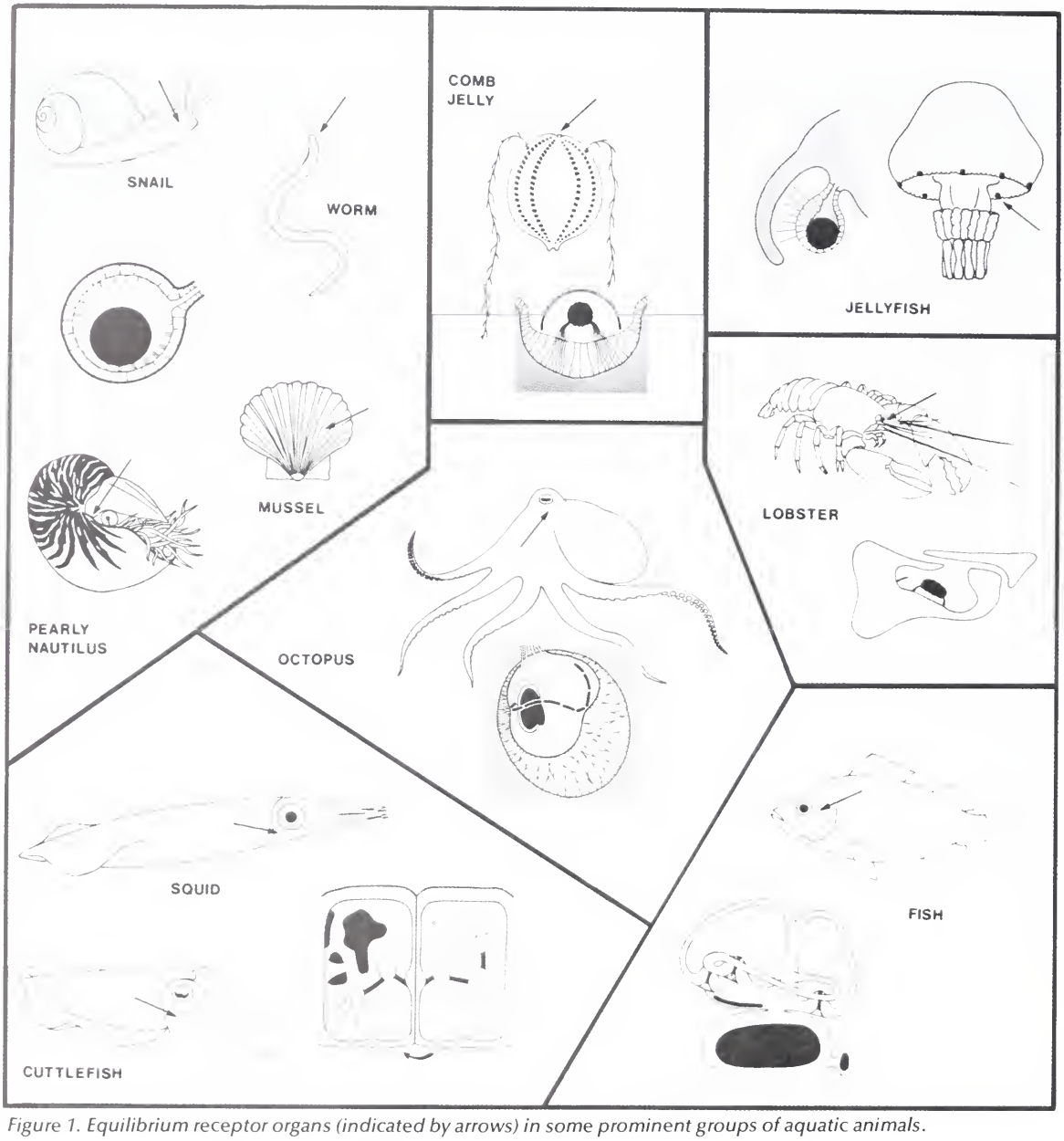


Figure 1. Equilibrium receptor organs (indicated by arrows) in some prominent groups of aquatic animals.

the neck moves like the statolith within the statocyst, and the water in the pan moves like the endolymph fluid (the stimulating mass in the angular acceleration receptors) within the statocyst.

The development of these two systems is well known in the case of the vertebrate's vestibular apparatus,* but is less understood in the invertebrate's statocysts. As a general rule, the more complex the animal's behavior in space, the more differentiated and specialized the sensory organs, and the more complex the associated neuronal and central nervous arrangements.

Cephalopod Equilibrium Receptor Systems

Twenty years ago, studies by the renowned English neuroanatomist J. Z. Young raised scientists' interest in cephalopod statocysts. Since then, these organs have become an outstanding example of the convergence of cephalopod and vertebrate sensory organs.

Although all cephalopods are marine, they do more than swim. Their complex behavior includes great maneuverability: they walk, leap,

*From the functional point of view, this separation is not clear. Recent experiments have shown that in cephalopods, crustacea, and some vertebrate species, the angular acceleration receptor systems at the level of their sensory cells are also sensitive to linear acceleration to a certain extent.

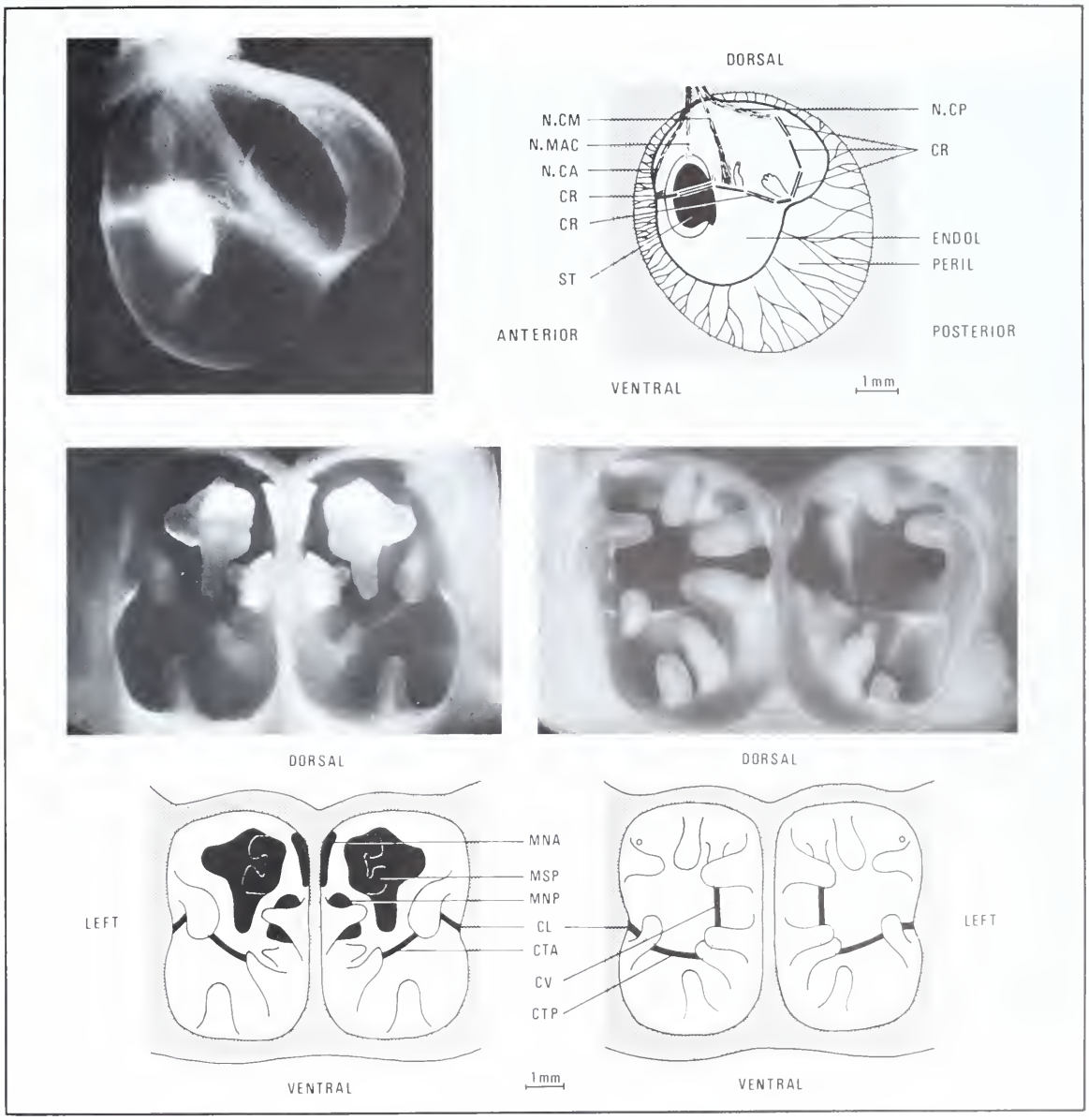


Figure 2. The equilibrium receptor organs (statocysts) of cephalopods. TOP: The statocyst sac (left), and whole left statocyst (right) of Octopus vulgaris. *CR = crista sections; ENDOL = endolymph-filled space; NCA, NCM, NCP, NMAC = statocyst nerves; PERIL = perilymph-filled space; ST = statolith on the macula. MIDDLE and BOTTOM: A section through the two statocysts of the cuttlefish* Sepia officinalis, *forward view (left) and rear view (right). MNA, MNP, MSP = the three maculae; CL, CTA, CTP, CV = the four crista sections. (From Budelmann, 1976)*

bury themselves, migrate, and some even perform short-distance flights. No wonder, then, that cephalopod statocysts (with the exception of the less maneuverable pearly nautilus) are highly developed equilibrium receptor organs that detect both linear and angular acceleration.

The statocysts are paired and are embedded separately in the cartilaginous brain capsule, below and on either side of the brain. In the two groups of higher cephalopods, the octopods (octopuses and nautiluses) and the decapods (such as cuttlefish and squid), each organ has the two structurally different sensory systems: 1) the gravity receptor system, consisting of plates of sensory cells (maculae) with their stimulating mass (statolith), of a higher specific weight than its surrounding fluid; and 2) the angular acceleration receptor system, made of ridges of sensory cells (cristae) with sail-like flaps (cupulae), using endolymph fluid as their stimulating mass (Figure 2).

The Gravity Receptor System

A closer look at the cephalopod's gravity receptor systems reveals a basic difference between the

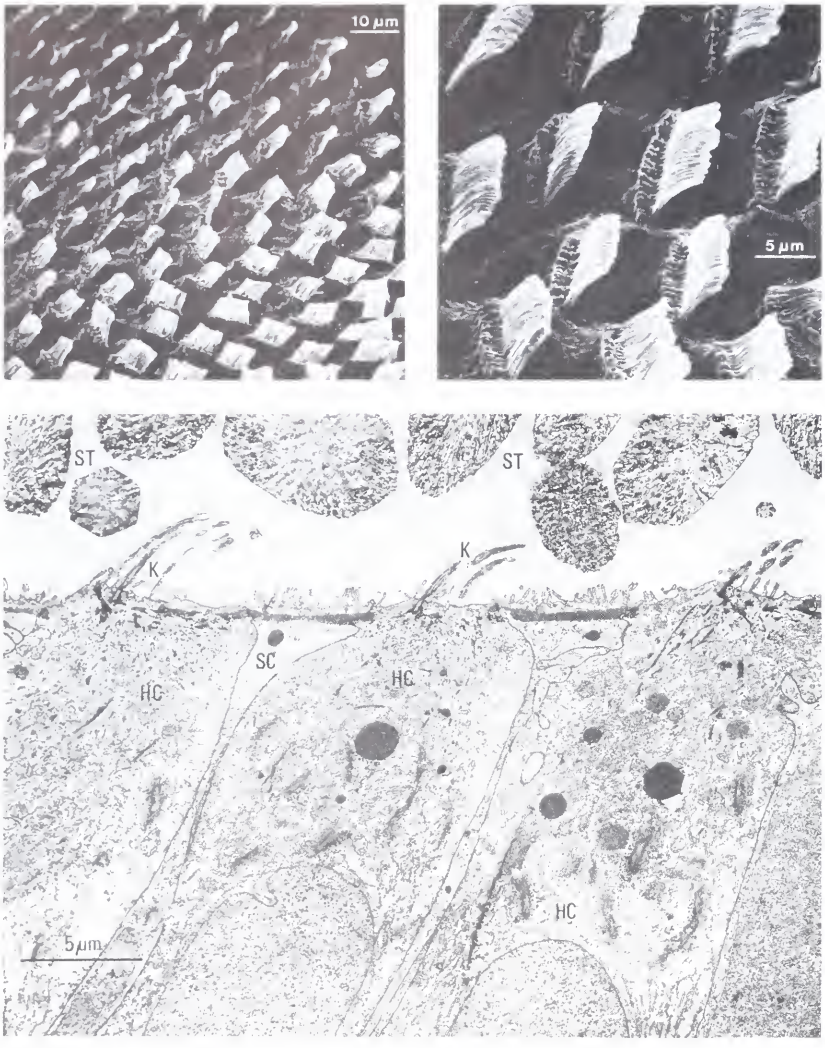
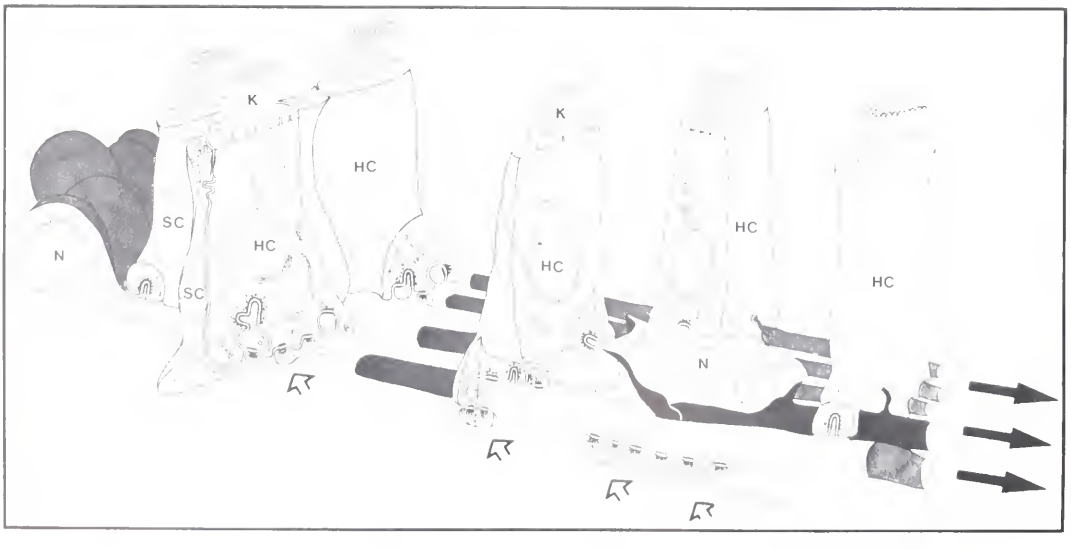


Figure 3. The sensory epithelium (macula) of the gravity receptor system in cephalopods. HC=hair cell; K=kinocilia; N=first-order afferent neuron; SC=supporting cell; ST=statoconia. TOP: Surface view (statolith or statoconia have been removed) showing the elongated kinociliary groups. (From Budelmann, 1979). MIDDLE: Hair cells, with kinocilia and statoconia. (From Budelmann, 1979). BOTTOM: Sensory hair cells and first-order afferent neurons in the octopus gravity receptor epithelium. Dark arrowheads indicate afferent (toward the brain) and open arrowheads indicate efferent (from the brain) information flow. (From Colmers, 1980)



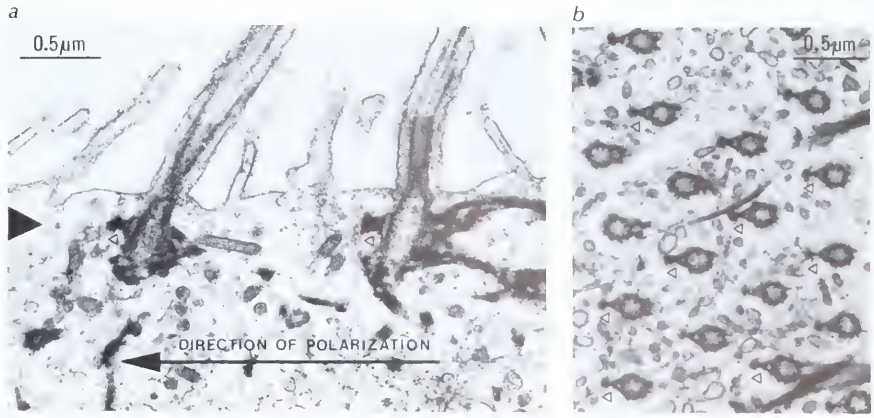


Figure 4. Polarization of the cephalopod sensory hair cells. (a) A section through the bases of two kinocilia of one hair cell, showing the orientation of their basal feet (open arrows). (From Budelmann, 1979). (b) A section through the basal bodies of some kinocilia in a hair cell (at the level indicated by the black triangle at far left), showing the uniform orientation of all basal feet in one cell (open arrows). (From Budelmann, 1979)

groups: there is only one such system in each octopod statocyst, whereas there are three in a decapod's.

Each macula is composed of between 1,000 and 5,000 receptor cells. Each of these cells holds up to 200 tiny hairs (kinocilia), and is thus called a hair cell (Figure 3). All the kinocilia of a single hair cell are arranged such that they form an elongated flap-like kinociliary group at the surface of the cell. The stimulating mass is attached to these kinociliary groups. When the receptor system is tilted, a local displacement (shear) of the stimulating mass occurs. This displacement then causes a small deflection of the kinociliary groups and thus stimulates the hair cells.

Each hair cell is polarized in a particular direction, which can be determined in a number of ways. The most obvious one is the position of the so-called basal foot structure at the base of each kinocilium; all basal feet of a single cell are oriented in the same direction (Figure 4), namely, at right angles to the rows of kinocilia. Also, the kinocilia do not stand straight up, but form an angle with the epithelium pointing away from the basal feet (Figures 3 and 4). These features make it possible to determine the direction of polarization of each hair cell, and thus to determine the pattern of polarization of the whole hair cell epithelium (Figure 5).

The movements of the stimulating mass across the sensory epithelium excite (depolarize) or inhibit (hyperpolarize) the hair cells in a complex pattern because of each hair cell's specific orientation to the motion (see page 29). Before reaching the brain, however, this pattern probably will be altered by first-order neurons, as can be surmised from the ultrastructural organization shown in Figure 3. In addition, they are modified at various levels by numerous signals that come from the brain. Whatever the final pattern of signals that reaches the brain, it yields the quantitative information regarding the animal's position.

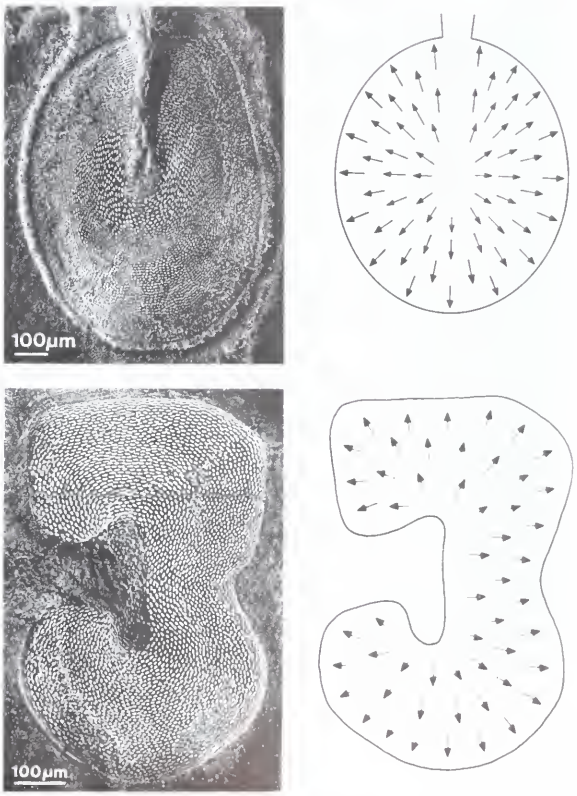


Figure 5. Two arrangements of kinociliary groups of hair cells at the surface of a gravity receptor epithelium (macula), and their corresponding patterns of polarization. Maculae of the statocyst of Octopus vulgaris *(TOP) and the cuttlefish,* Sepia officinalis *(BOTTOM). (From Budelmann, 1976, 1979)*

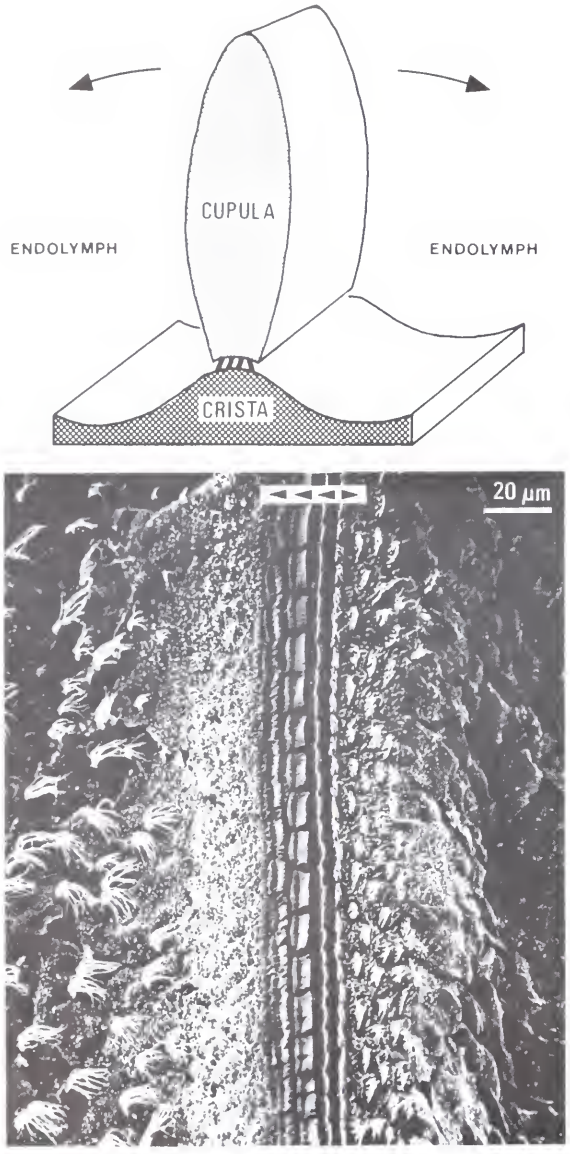


Figure 6. The angular acceleration receptor system of the cuttlefish Sepia officinalis. *TOP: The sail-like cupula moves like a swinging door. Angular acceleration stimuli applied to the system will cause the endolymph to move, and thus cause the cupula to deflect, in a direction opposite to that of acceleration. BOTTOM: Crista section (with cupula removed), showing the regular arrangement of the kinociliary groups in four rows of hair cells. Arrows indicate direction of polarization in each row.*

The Angular Acceleration Receptor System

The design of the cephalopod's angular acceleration receptors is basically similar to its gravity receptors. In both octopods and decapods, again, hair cells are the receptors that form the sensory epithelium (crista). Like a ridge, the crista winds over three planes almost perpendicular to one another. As in the gravity receptors, each hair cell bears numerous kinocilia, which form an elongated kinociliary group at the surface of the cell (Figure 6 and 3). And again, each hair cell is polarized structurally and functionally in one direction (Figure 4).

The crista ridge is divided into several sections, each of which contains a cupula attached to the hair cells. This sail-like, delicate structure protrudes freely into the fluid-filled statocyst cavity (Figure 6). In the crista/cupula system, angular acceleration will result in a movement of the fluid relative to the crista (as in the example of water in a pan, cited earlier). The cupula is then bent by this fluid movement and thereby causes the kinociliary groups to shear in one or the other direction, depending on the direction of acceleration. This shearing either excites or inhibits the hair cells, depending on their polarization.

Behavioral Reactions

What kinds of behavioral reactions in cephalopods are influenced by the various equilibrium receptor systems? In the octopus, the destruction of one of the two statocysts has little effect as long as the animal is walking around. However, when swimming, the organism deprived of one statocyst is disoriented and rolls to the affected side around its longitudinal axis. In the cuttlefish, this effect is even more obvious; the animal permanently spins around, making about two rotations per second.

The function of the two statocysts becomes clearer after both organs have been destroyed. The octopus becomes noticeably unsteady, but still can walk. It spreads its arms to get as much stability as possible, using its suckers to adhere to the substrate. Experiments with animals that are subsequently blinded show that this walking is largely guided by sight, because their few movements become even more uncertain. Swimming, of course, is more affected than walking; the animal zigzags, corkscrews, and somersaults irregularly. Like the cuttlefish, the octopus is completely disoriented.

We can distinguish between behavior that is steered by gravity and that which is steered by angular acceleration by examining the two kinds of compensatory eye movements exhibited by the animals: counter-rolling and rotational nystagmus. When an animal's spatial orientation changes, it tries to keep the position of its eyes constant with respect to gravity, thus stabilizing the retinal image of the visual world around it. This reaction is called

counter-rolling, and can easily be seen in cephalopods. For instance, the octopus pupil remains nearly horizontal, whatever the body position (see front cover photograph).

Counter-rolling eye movements have been studied in octopuses and cuttlefish that, without visual cues, were slowly tilted throughout a full-circle while avoiding stimulation of angular acceleration receptors. This causes movement of the stimulating mass over the sensory epithelium. This movement varies in direction and strength. The animals try to counter-roll their eyes throughout a 180-degree rotation, but of course cannot. (An unrestrained octopus, for example, can counter-roll its eyes for at least 60 degrees to either side.) Destruction of the gravity receptors on one side reduces the compensatory counter-rolling, and destruction of the receptors on both sides eliminates it completely, indicating that this behavioral reaction depends on the function of the gravity receptor organs alone (Figure 7). The same is true for the cuttlefish, as could be shown by a step-by-step elimination of its six gravity receptor systems. In detailed experiments on octopus, when with a centrifuge the pull of gravity is changed but not its direction, the degree of compensatory eye movement is not affected. This shows that the compensatory counter-rolling in the octopus is responding only to changes in direction, not strength. In vertebrates and crustacea, however, both direction and strength of movement of the stimulating mass cause changes in compensatory eye movement. This difference in function does not reflect a different receptor cell function, but results from differences only at the level of the brain.

The other compensatory eye movement, rotational nystagmus, can be demonstrated by placing an octopus on a moving horizontal turntable and exposing it to angular acceleration. The animal tries to keep the image of the outside world stable on its retina (even without visual cues or when blinded). This means it moves its eyes against the direction of acceleration. When the turntable is stopped abruptly, the octopus shows postrotational eye flicks (nystagmus). These behavioral experiments, as well as electrophysiological ones, have shown that the function of the angular acceleration receptor

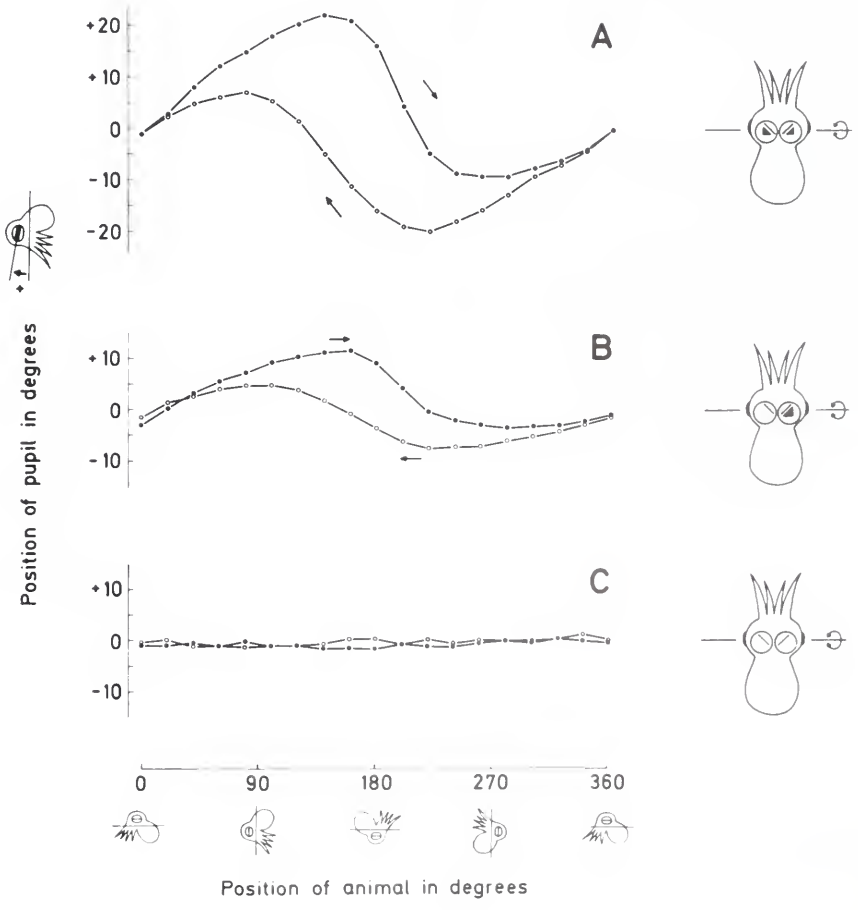
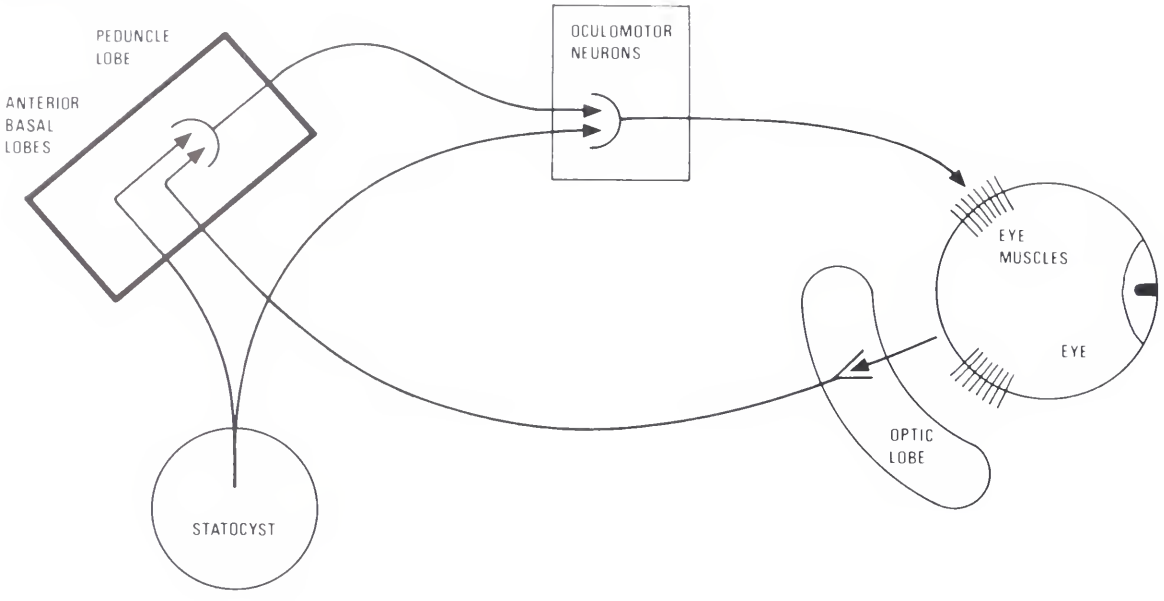


Figure 7. Compensatory counter-rolling of the eyes of an octopus, as a function of its body position relative to gravity during rotation around its transverse body axis. Arrows indicate the direction of tilt. (A) shows reactions of a normal animal; (B) an animal with one gravity receptor system destroyed; and (C) one with both gravity receptor systems destroyed. (From Budelmann, 1975)

CEPHALOPODS



VERTEBRATES

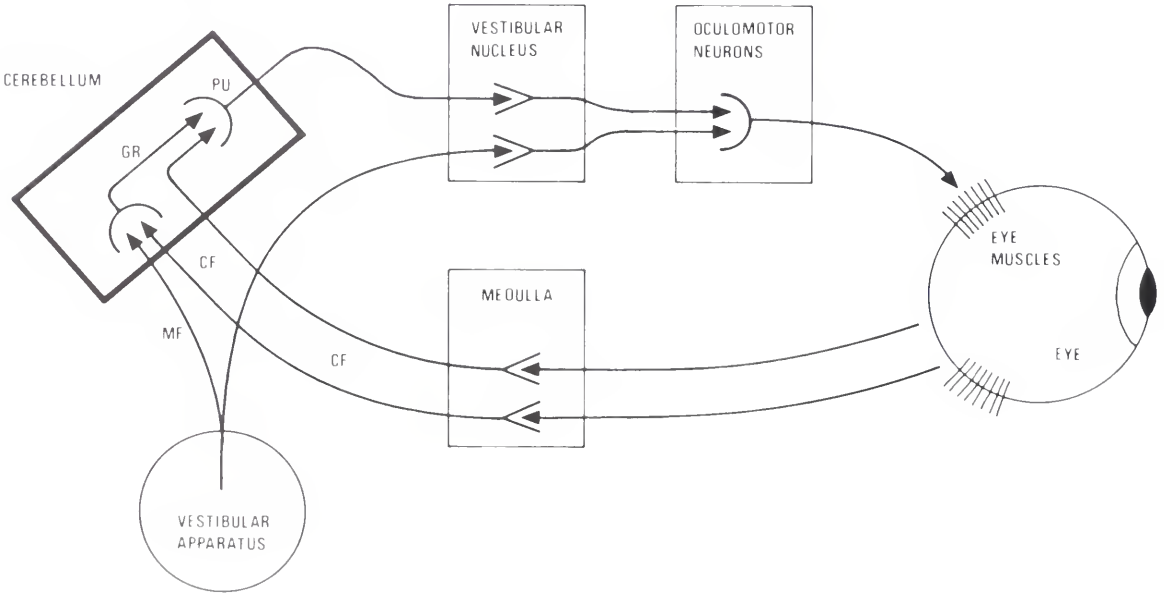


Figure 8. Similarities in brain connections for oculomotor control in cephalopods and vertebrates. CF=climbing fibers; GR=granule cells; MF=mossy fibers; PU=Purkinje cells. (Adapted from Young, 1976. Reprinted by permission from Nature, Copyright 1976, Macmillan Journals Limited)

systems in cephalopods is basically similar to that of corresponding vertebrate systems.

Oculomotor Control and Behavior

The complex neural reflexes that keep eye position constant while the animal's body moves about are an essential component of visually guided behavior. This is true for humans as well. Imagine that we are aiming at a target under any kind of circumstances: using a bow and arrow, striking by hand, cleaving a diamond, pointing at the horizon. We fix the target visually and then somehow preprogram — from past experience — our motor neurons for the behavior to be performed, using our eye position as reference. If during this process our body is solidly planted on a stable platform and we do not move our eyes, the fixed point remains stable and we may succeed in hitting the target. If, however, we stand upright and thus sway slightly, or if there is a gusty wind, or if we are aboard a small boat in the waves, our target would become impossible to fix visually. Its image would wildly cross over the retina of our eye, and performing any visually guided behavior would become impossible, were it not for the oculomotor control reflexes.

These reflexes utilize information from the gravity and angular acceleration detectors telling them how much movement the body is undergoing. They then feed this information — analogous to a negative feedback servomechanism — to the eye muscles, so that body movements, which in a fixed eye produce a target image shift on the retina of, say, 10 micrometers to the right, immediately cause an eye movement equivalent to an image shift of 10 micrometers to the left. In other words, the target image remains in the same position on the retina. Even complex movements of the body are carefully measured, translated, and sent to the eyes to provide the eye stability needed to perform visually guided behavior. To truly understand the function of the oculomotor control system, one must also consider other inputs, such as from proprioceptors, vision, and higher integration centers.

Vertebrates have a large part of their brain devoted to the fine tuning of their movements, including oculomotor control. This area is the cerebellum. In cephalopods, the oculomotor neurons of the eye muscles get their statocyst input via two pathways: directly, and indirectly via higher integration centers in the brain (the peduncle lobes and anterior basal lobes), where visual information concerning eye position and movement is added (Figure 8). These higher centers are known to cause various motor defects after their extirpation, and can be compared with the vertebrate cerebellum.

Conclusion

The remarkable convergence between vertebrate and cephalopod equilibrium senses underscores one important biological rule. The physical forces (here linear and angular acceleration) that need to be measured exert a shaping power on the biological receptor organs, leading to great similarities in their overall structure, including the design of the neural steering circuits of the brain. Despite profound differences between the neural organization of vertebrates and invertebrates, the two groups seem to have been forced to adapt similar organs and brain centers in cases where they have to optimize their use of physical and chemical stimuli in the environment. Similar convergent evolution is seen in the wings of birds and bats, in the smell and taste receptors of lobsters and catfish (see page 4), and in the eyes of vertebrates and cephalopods (see page 19). The need to optimize may have been forced upon the cephalopods in their competition with fishes.

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Acknowledgments

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Electroperception

Organisms have adapted to different environments and evolved sense organs that respond selectively to particular forms of energy. Because we lack specialized receptors, we are "blind" to weak forms of electric and nonphotic electromagnetic energy that surround us constantly. The shocking experience with a faulty electric outlet is not mediated through an electric sense but through direct stimulation of the nervous system.

Elephantfish, Gnathonemus petersii. *At right, elephantfish swimming in a tank.*

The underwater environment is packed with electric and electromagnetic events. If we were able to sense this electric environment, a whole new world would reveal itself: weak electric fields emanate from many aquatic organisms, especially from fishes and wounded crustaceans, and to a lesser extent from mollusks, starfish, and sponges. In most cases, we would feel direct current (DC)* voltage gradients that in the ocean range from as low as one hundred millionth of a volt per centimeter to as large as one hundred thousandth of a volt per centimeter. In freshwater, the voltage gradient is about one hundred times greater. We would also detect alternating current (AC)** voltage gradients associated with an organism's movements, breathing, or locomotor behavior. Soon we would discover that many inanimate objects produce DC fields, their interface with water acting as a battery. Lightning discharges and man-made radio waves are sources of electric noise pollution that certainly would not escape our underwater electric ears or eyes. Blaxter has said (see page 28) that sound "has much to recommend it as a form of sensory stimulus." So, too, does electric energy, and nature, not surprisingly, has exploited it.

A number of aquatic organisms have evolved specialized receptors with which they are able to perceive many aspects of the underwater electrical world. Another group of electric signals in an aquatic environment are supplied by species that have evolved the ability to generate their *own* electric energy which they use in predatory, orientation, and communication behavior.

Electric Signals in Water

Let us for a moment contemplate the fate of an electric signal underwater and compare it with other energy forms. The conduction of electric signals in water is almost instantaneous and thus comparable with that of visual ones. Acoustic, mechanical, and chemical stimuli travel considerably slower. Like sound, an electric signal does not persist once it is discontinued; both types of signals, then, differ from chemical stimuli, which can linger for quite some time. Turbid water and darkness do not impede the transmission of electric, acoustic, chemical, and mechanical signals but do restrict visual ones. Dense vegetation, submerged trees, roots, and even small rocks present barriers to visual stimuli, but are not obstacles to electric currents, which can go around them.

As animal behaviorists, we are concerned with the biologically meaningful range within which such a stimulus can affect the sense organs of another organism when the stimulus is no longer clouded by environmental noise, thus serving in social communication and orientation. To assess such a biologically effective range we must look at the amount of emitted or available stimulus energy, the sensitivity of the receptors involved, the spherical spread of the signal, and the attenuating effects of the surrounding medium on the transmission of the stimulus.

We have studied the effective range of electric signals in weak-electric fishes (Table 1), which are characterized by their ability to emit and perceive weak electric discharges. In contrast to the admirable long-distance performance of acoustic sensory stimuli (up to several hundred kilometers), the range of the electric sense in mormyrids* is restricted to a humble 100 centimeters for electrocommunication and a mere 10 centimeters for electrolocation (Figure 1).

The effective ranges of the organism's electric sense in electrolocation and electrocommunication were found to vary with several factors — including species, body shape, and electrical resistance of the fish's skin; physical and electrical properties of the object; and, most important, conductivity of the surrounding water, that is, the degree of its dissolved ionic material. The optimal ranges of 10 and 100 centimeters are associated with low levels of water conductivity that conform well with measurements taken in the fish's natural habitats.** Even over short distances, the organism is supplied with enough electrical information to avoid obstacles, maintain proximity to conspecifics, and compromise with extraneous electric noise.

Electroreceptive and Electrogenic Fishes

There are two groups of fish species distinguished here (Table 1): those which have evolved electroreceptors only (electroreceptive fishes) and those which, in addition, have evolved specialized electric organs capable of generating electric discharges (electroreceptive and electrogenic fishes). Species in the first category sense electric fields that are not self-generated, but rather, are produced by other sources in the environment (passive electrosensory group). Species in the other category also sense electric fields that they actively generate themselves (active electrosensory group). Both groups have representatives among the

*An electric current flowing in one direction only and substantially constant in value.

**An electric current that reverses its direction at regularly recurring intervals.

*A family of African freshwater fish (members of the order Mormyriformes), many of which are distinguished by their long, tube-like snouts.

**Less than or equal to 100 micro-Siemens per centimeter compared with distilled water, which is 0 micro-Siemens per centimeter, and New York City tap water, which is 70 micro-Siemens per centimeter.

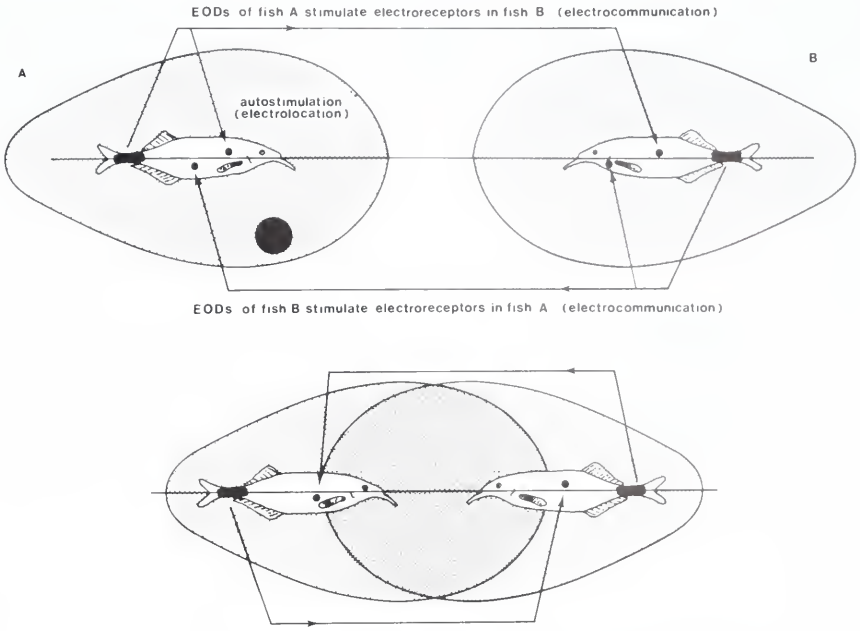


Figure 1. Ranges of electrocommunication and electrolocation in mormyrid weak-electric fishes. The "bubble" around the fish indicates the extension of the electrolocation field to about 10 centimeters. The presence of an object (black dot in upper figure) or the fishes themselves (lower figure) will be electrically "felt" by the fish emitting the electric discharge. The electrocommunication range is almost 10 times larger than the electrolocation range.

cartilaginous and bony fishes and can be found in both marine and freshwater environments.

Electroreceptors

An electroreceptor is a sense organ that responds selectively to natural electric fields. We use both electrophysiological recordings and behavioral tests to determine whether a particular sense organ functions as an electroreceptor. Most known electroreceptors are related to the lateral-line organs (see page 27) (which are water vibration receptors characteristic of all fishes) and are of two types — ampullary or tuberous organs (Figure 2).

The ampullary receptor consists of a flask-shaped ampulla embedded beneath the surface of the skin. The bottom of the ampulla contains the sensory cells which are in contact with the outside through a jelly-filled canal. In sharks, rays, skates, and marine catfish, in which the ampullary organs are called ampullae of Lorenzini (after the man who first described them in the 17th century), these canals may be as long as one-third of the organism's body (see Figure 4, p. 58). In contrast, in all electroreceptive freshwater fishes these canals are short, often microscopically so.

Ampullary organs are the more sensitive electroreceptors. Sharks and skates respond to stimuli as low as 0.01 microvolts per centimeter, which would correspond to a voltage gradient set up between the poles of a flashlight cell placed more than 1,500 kilometers apart. Sharks within close range of prey are particularly sensitive to the electric fields around aquatic animals. In some electrogenic mormyrid species, the ampullary receptors also respond to the fishes' own electric

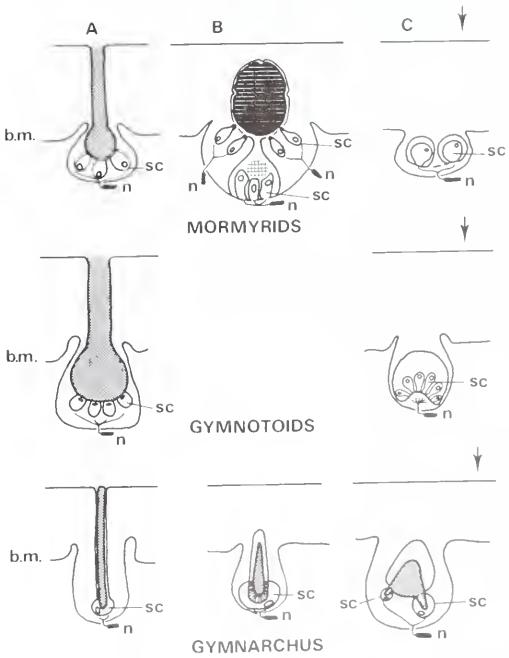
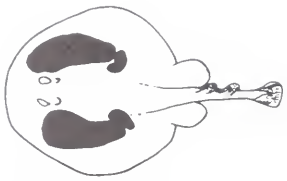
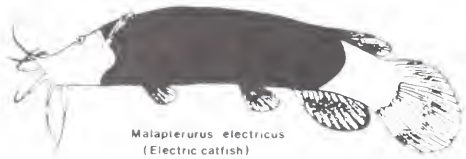


Figure 2. Typical electroreceptors in weak-electric fishes. The ampullary organs (A) respond predominantly to DC electric fields and to low-frequency stimuli emanating from many aquatic organisms, but also to the fish's own electric discharge. The tuberous mormyromasts (B) serve in electrolocation and the tuberous knollenorgans (C) in electrocommunication. Shaded areas represent jelly-like material; sc, sensory cell; bm, basement membrane; n, nerve. Arrow indicates fish's body surface. (From Szabo, 1965, Journal of Morphology, courtesy of Alan R. Liss, Inc.)

Astroscopus y-graecum
(Stargazer)

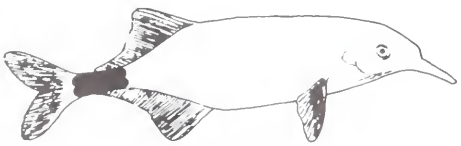


Torpedo marmorata
(Marbled electric ray)



Malapterurus electricus
(Electric catfish)

Gymnotus carapo
(Knifefish)



Gnathonemus petersii
(Elephantfish)

Figure 3. Electric organs have evolved independently in several groups of marine and freshwater fishes. In most cases these organs develop by modification of muscles in various parts of the fish's body (darkened areas).

ELECTRORECEPTIVE FISHES (without electric organs)		
marine	CHONDRICHTHYES (cartilaginous fishes)	ELASMOBRANCHII (AL) SQUALIFORMES (sharks) (AL) RAJIFORMES (all ordinary rays and skates) HOLOCEPHALI (AL) Chimaeridae, *Hydrolagus colliei* (rat fish)
marine	OSTEICHTHYES (bony fishes)	(AL) SILURIFORMES Plotosidae *Plotosus anguillaris* (marine catfish)
freshwater	CHONDRICHTHYES	(AL) RAJIFORMES (Myliobatoidei) Potamotrygonidae, *Potamotrygon circularis* (S. American freshwater stingray)
freshwater	OSTEICHTHYES	(AR) ACIPENSERIFORMES Polyodontidae (chondrostean paddlefish) (AR) SILURIFORMES Ictaluridae; Siluridae, *Kryptopterus* (catfish) (AR) DIPTERIFORMES (Dipnoi) *Protopterus dolloi* (lungfish) (AR) BRACHIOPTERYGII (reedfish and bichirs)

Table 1. Electroreceptive and electrogenic fishes.
Types of electroreceptors: (AL), ampullae of Lorenzini; (AR), ampullary receptors; (TR), tuberous receptors; (N), electrosensitivity not investigated.

ELECTRORECEPTIVE and ELECTROGENIC FISHES
(with electroreceptors and electric organs)

Strong electric organ discharges (EODs)

Type III "volley species"
Intermittent, 2 to several hundred discharges

(EODs serve in defensive and predatory behavior)

(AL) TORPEDONOIDEI Torpedinidae
Torpedo marmorata, T. nobiliana
(electric rays)

(N) PERCIFORMES Uranoscopidae
Astroscopus y-graecum
stargazer)

Malapteruridae
Malapterurus electricus
(African electric catfish)

Weak electric organ discharges (EODs)

(AL) Rajoidei, Rajidae, *Raja*
(electric skates)
(Significance of EODs unknown)

Type II "pulse species"
Continuous, less than 1 to about 100 Hz

Type I "wave species"
Continuous, from about 100 to 1,800 Hz

(EODs serve in electrolocation and electrocommunication)

AFRICAN SPECIES
(AR, TR) MORMYRIFORMES
Mormyridae
(>200 species)

Gymnarchidae
Gymnarchus niloticus

S. AMERICAN SPECIES
(AR, TR) CYPRINIFORMES (Gymnotoidei)
Gymnotidae
Rhamphichthyidae
(S. Amer knifefishes)

Apteronotidae
(S Amer knifefish)

Electrophoridae
Electrophorus electricus
(electric eel)

discharge, but only under low water-conductivity conditions where electrolocation and electrocommunication performances appear to be most effective.

The tuberous receptor consists of an epidermic capsule containing sensory cells with no direct connection to the exterior. Tuberous organs are up to 10,000 times less sensitive than ampullary receptors and have exclusively evolved in the electrogenic, weak discharge-generating fishes (Figure 2). Here, each electric discharge affects two types of tuberous receptors, the mormyromasts and the knollenorgans. As a class they respond optimally to stimulus frequencies from 60 to 1,800 Hertz (Hz). For a particular species, however, the range of optimal frequency sensitivity is limited and species specific.

Electric Organs

The ability to generate and emit electric discharges has evolved independently in a small number of marine and freshwater fishes (Table 1). The electric discharge is produced by an organ consisting of several columns of flattened cells, the electroplates or electrocytes, whose embryonic origin has involved the modification of certain muscle groups: the eye muscles in the stargazer, branchial muscles in the torpedinid rays, pectoral muscles in the electric catfish, and axial and tail muscles in the Neotropical gymnotoid knifefishes and the African mormyriforms (Figure 3). (The exception is the South American gymnotoid Apteronotidae, whose electric organ is derived from nerves.) Like muscle fibers, the electrocytes are innervated by motoneurons that depolarize simultaneously, thereby generating an electric organ discharge (EOD) whose waveforms are species-specific characteristics.

It has been customary to distinguish between strong and weak EOD-emitting fishes (Table 1). The EODs from electric eels, marine torpedoes, and African electric catfish are so powerful that they can stun and even kill passing prey fish. Baby catfish of 2 centimeters can produce up to 10 volts, sufficient to prey on tadpoles; large electric catfish and electric eels can generate several hundred volts; and torpedoes can produce up to 50 amperes. The electric organ discharges in all strong-electric fishes thus function as defensive and predatory weapons. There is some evidence that the EODs also serve in locating prey (in the electric catfish) and as signals in social communication (in the electric eel and catfish).

Strong-electric fishes do not continuously emit EODs but intermittently generate volleys consisting of from two to several hundred individual discharges. In field observations, the nocturnal electric catfish was seen to produce significantly more and longer-lasting volleys during the night than during the day. The volley-type

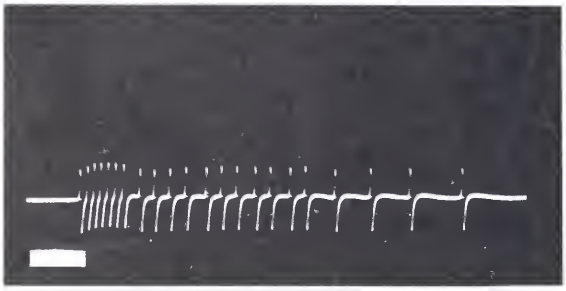


Figure 4. Electric organ discharges from an African electric catfish. Time mark: 20 milliseconds.

repetition rate illustrated in Figure 4 is characterized by an initial period of short interdischarge intervals (approximately 2 milliseconds) which gradually increase in duration (up to more than 100 milliseconds).

Weak electric organ discharges that are generated by the freshwater gymnotoids and mormyriforms are too small to aid in offensive or defensive behavior. It was H. Lissmann of Cambridge University who in 1958 proposed that the weak EODs aid the fish in object location and social interaction.

The Electric Sense in Weak-Electric Fishes

Ryan (see page 55) discusses the electric sense as it pertains to sharks, skates, and rays. I will focus on the electric sense in weak-electric fishes and illustrate its role in electrolocation and electrocommunication.

Two major groups of unrelated freshwater fishes are both electroreceptive and electrogenic. The South American knifefishes are characterized by an elongate body and anal fin; the electric organ runs almost the entire length of the body. In the African mormyriforms, one species, *Gymnarchus niloticus*, possesses an elongate body with a long dorsal fin. The mormyrids are diverse in body shape, reflecting their adaptation to a great variety of habitats. The electric organ is always located in the tail (Figure 3).

Each time a fish emits an EOD, an electric field propagates from the fish. To map the electric fields we have to take snapshots. At the height of each discharge we determine the positions around the fish where the electrical potential between a measuring electrode and a distant reference electrode remains constant. Figure 5 illustrates such lines of equal potentials (isopotential lines). The physicist will tell us that in a large volume of water the fish's electric field resembles that of a dipole field when measured at distances that are long compared to the length of the fish. Within close range, owing to the animal's body shape, the field differs considerably from an ideal dipole field.

Because of the instantaneous conduction time of the electric signal, time differences between

emission and reception of the signal could hardly be exploited by the fish in locating objects, as is the case with organisms producing sound signals with about 20,000 times slower conduction time (see page 27). Object location in weak-electric fishes works differently.

Electrolocation

Any object whose conductivity is different from the surrounding water, such as a metal or plastic rod, or another fish, will distort the fish's self-generated electric field. For example, objects with conductivities lower than that of the water lower the density of the electric field lines in an area of the fish's skin that is nearest to the object. On the other hand, objects with higher conductivities increase the density of electric field lines. Electrophysiologists have studied these changes in current density and found that the presence of, say, a plastic object results in a decrease of the receptor's "firing rate" — the process of sending coded neural messages to the brain — whereas the presence of a metal object results in an increased receptor response.

The tuberous electroreceptors involved in electrolocation are scattered throughout the fish's body surface. The presence of an object will therefore affect some receptors more than others. From the mosaic of local receptor responses, the fish may obtain information about the object's position and its electric nature. We could say that such an object casts its electric image on part of the fish's body wall.

To enhance an electric image, fishes have developed several peripheral focusing strategies, analogous perhaps to the accommodation response of a lens to nearby objects. Gymnotoids, while exploring a novel object, often bend their tail (containing the electric organ) around it. Many of the South American knifefishes have tail filaments several times longer than the body. These filaments considerably extend the range of electrolocation in the tail region. By swimming backward into

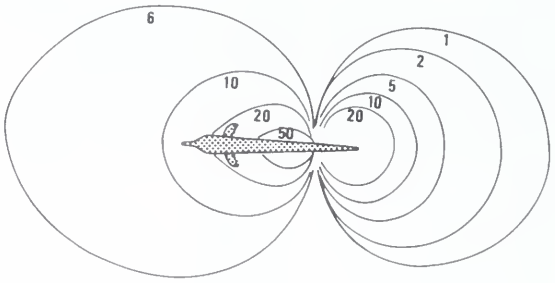


Figure 5. The electric field generated with each electric organ discharge propagates in all three dimensions and can be visualized as a bubble around the fish expanding almost at the speed of light. Isopotential lines (drawn in one plane only) show the extension of such an electric field. Values are given in microvolts per centimeter. (From Boudinot, in Szabo, 1977, courtesy of Springer-Verlag)

prospective shelters, holes, and crevices, the fish maximizes the electric image the surroundings cast on the body wall. Mormyrids, which with some notable exceptions do not have long tails and whose electric organ is restricted to the tail, improve on the electric image of a nearby object by probing it. At well-defined distances, in the presence of novel stationary objects, the fish displays tail bending — lateral and/or tangential motor probing acts. When the fish moves rapidly backward and forward along the object, a maximum number of electroreceptors are optimally affected and thus the electric image is improved. When we try to see and locate a difficult visual target our heads move in a similar way.

In addition to having a motor response, the fish has an electric focusing strategy. While probing an object it accelerates its variable and low EOD repetition rate to a stable and higher level (Figure 6). An increased EOD rate means more receptor responses and thus more information sent to the brain per EOD and time unit. Immediate distortions of the self-generated field aid the fish in close-range, local orientation. Several mormyrid

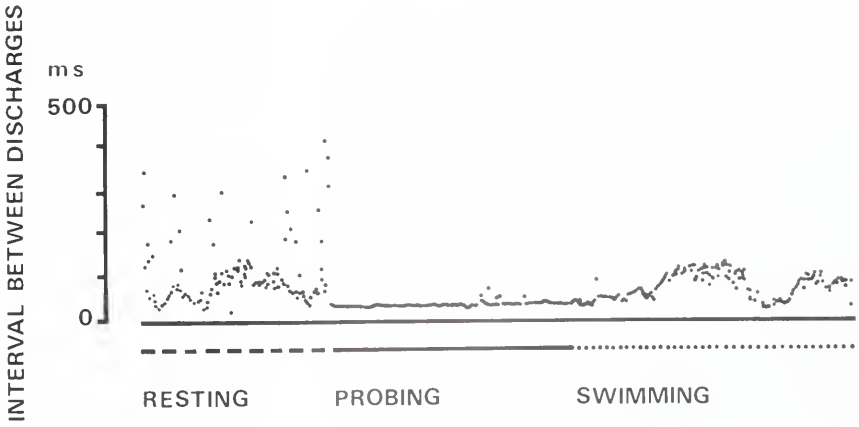


Figure 6. Electric organ discharges from a mormyrid fish, Marcusenius cyprinoides, *during resting, object probing, and swimming. The duration of the consecutively plotted intervals between discharges indicates how the variable resting activity became regular during probing with a stable interval of 28-30 milliseconds. (Courtesy of M. J. Toerring)*

species are seasonal migrants and others show daily migratory patterns from large rivers into small creeks and vice versa. One may speculate that because the fish learns and later remembers the electric images cast upon its body during migration, the active electric sense may play a supporting role in long-range orientation.

Electrocommunication

What do we expect a communication system to accomplish? Basically, two broad classes of information must be transmitted: identity information (species, sex, developmental stage or age class, and individuality); and motivational information (reproductive readiness, threat, and submission).

The same EODs that weak-electric fishes use in electrolocation can stimulate members of their species and other species at much greater distances; they can thus serve as signals in social communication. In fact, the specific temporal patterning of EOD activity during social encounters in fishes has led researchers to suggest that it is analogous to bird song, with a similar variety of functions, such as mate seeking, territorial defense, and other social and orientation roles.

Weak-electric fishes have evolved different strategies for "electrically" transmitting identity and motivational information. Among mormyriform and gymnotoid fishes we distinguish two types of electric discharge rhythmicity (Table 1). Type I "wave species" emit nearly sinusoidal EODs at extremely stable repetition rates ranging from 100 to 1,800 Hz. These stable frequency bands are species specific.* Type II "pulse species" have considerably lower EOD repetition rates ranging from less than 1 Hz to 140 Hz. In many gymnotoid pulse species the EOD rate remains stable. In mormyrids, on the other hand, the repetition rate is quite variable most of the time. In contrast to the wave species, pulse species show a wide interspecific overlap in the species-typical ranges of EOD repetition rates.

Identity Information

Wave species broadcast within species-specific frequency bands. In mormyrid pulse species, identity information is coded with the characteristic waveform of the individual discharge. Figure 7 shows species-specific differences related to the duration as well as amplitude and polarity of the different phases of the single EOD. To test the hypothesis that individual EODs (in pulse species) and stable frequency bands (in wave species) are important cues in species recognition, we played recordings of species-specific and modified,

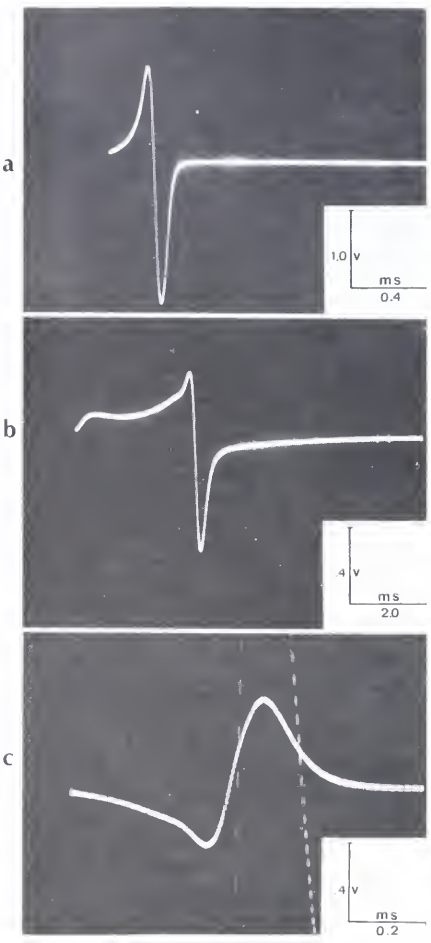


Figure 7. Individual mormyrid electric organ discharges. Waveform is a species-typical characteristic: (a) Marcusenius paucisquamatus*; (b)* Marcusenius conicephalus*; (c)* Mormyrops zanclirostris.

computer-generated signals to the fish. Under these conditions, the receiver fish's electroreceptors responded optimally and the fish was optimally attracted to the source of those signals which exactly simulated the species-specific waveform and/or rhythmicity.

To signal maleness or femaleness some species have developed characteristic differences in their EOD frequency bands or waveforms. Male gymnotoid *Sternopygus macrurus* broadcast within a 50-90 Hz range and females within 100-150 Hz. Figure 8 illustrates the striking sexual difference in the waveforms of a mormyrid pulse species. Sexual differences in electric signaling serve in mate attraction and courtship behavior.

Characteristic differences related to age class were found in juveniles of *S. macrurus*, which emit an EOD frequency of around 80 Hz, an intermediate

*Examples include gymnotoids such as *Sternopygus macrurus*, 50-150 Hz; *Eigenmannia virescens*, 240-625 Hz; and *Apteronotus albifrons*, 750-1,250 Hz; and mormyriforms such as *Gymnarchus niloticus*, 200-450 Hz.

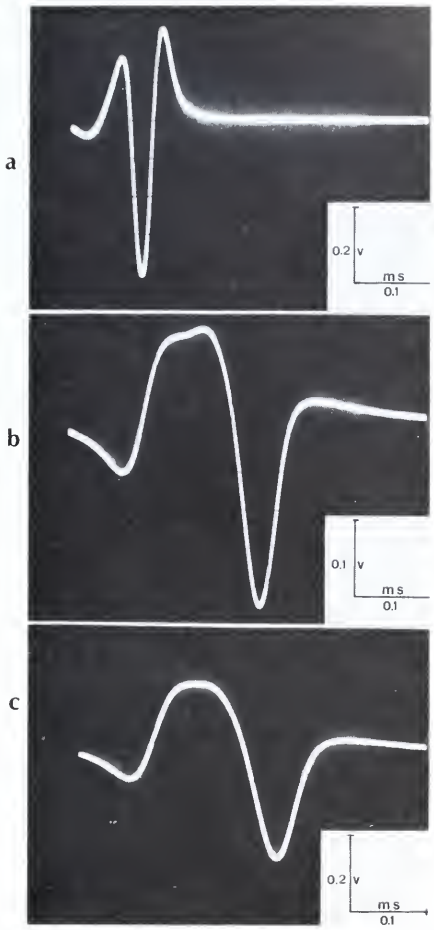


Figure 8. Sex difference in the waveform of the individual discharge of the mormyrid Stomatorhinus walkeri. *(a) female, (b) male, and (c) juvenile male. (The same waveform also has been attributed to* S. corneti; *C. Hopkins, in press.)*

between their parents' frequencies. Correspondingly, juveniles of some pulse species generate intermediate waveforms (Figure 8). Larval mormyrids emit an EOD that is first generated by a larval electric organ eight days after hatching. After about six weeks, when the definitive tail organ becomes functional, the larval discharge is gradually replaced by the differently shaped adult EOD. It may be that larval EODs serve in signaling identity to the parent fishes and maintaining group cohesion among the larvae.

We noted earlier that the EOD repetition rate in mormyrid pulse species is quite variable with regard to the average interval maintained between successive discharges. If we look at the distribution of these intervals over a longer period of time (let us say, 10 to 20 minutes), we discover characteristic modal distributions, which in some mormyrid

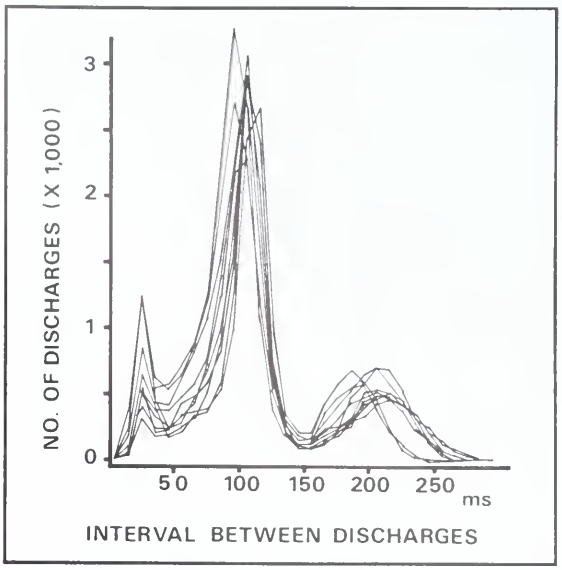


Figure 9. Electric organ discharges from the mormyrid Gnathonemus petersii, *recorded on 10 different days (during daytime). The distribution of inter-discharge intervals remains remarkably stable. Other conspecifics have different "fingerprints." (Courtesy of D. Malcolm)*

species are individual-specific "fingerprints" (Figure 9). We do not yet know whether such fingerprints are actually being used in individual recognition among members of a given species.

Motivational Information

The modifiability of EOD rhythmicity (that is, the temporal sequence of EODs) and the fish's immediate EOD-responsiveness to a variety of stimuli, including electric, magnetic, optic, mechanical, thermal, and chemical, have made EOD rhythmicity changes prime candidates for transmitting motivational information. In both mormyrids and gymnotoids we find characteristic relationships between overt behavior and EOD activity. The behavioral situation and the social status of a pair of interacting individuals affect whether the pulse fishes rapidly increase their baseline frequency, decrease their activity, or cease discharging altogether for various lengths of time. In addition, the variable interval between discharges may temporarily become extremely stable at a given frequency level or alternate between two intervals of fixed duration. In the gymnotoid wave species, different types of sharp EOD rate increases and discharge cessations (breaks) were observed during social encounters and were related to threat, attack, submission, and courtship behavior.

Comparable with procedures testing the transmission of identity information, play-back experiments have convincingly demonstrated that motivational information is transmitted via

particular EOD activity patterns. For example, when an electric dipole mimicking the fish's electric organ is concealed in a plastic model fish, it is attacked less often when it broadcasts resting activity than when it emits an "attack pattern." Similarly, male *S. macrurus* respond to playback of female EOD patterns with typical frequency increases and EOD cessations, but do not respond to male EOD patterns.

During social encounters, two fishes could potentially jam each other's signals. The outcome of such jamming should be similar to the result of two people talking to each other at the same time: the information exchange is close to zero. When the fishes, under laboratory conditions, were subjected to coincident discharges or identical frequencies (emitted by an electric dipole in a model fish) they failed to locate nearby objects. If we want to understand our neighbor's comments we stop talking and listen before responding. Under natural conditions, pulse species avoid jamming — one fish places its own discharge at a fixed delay following the other's discharge in a kind of waiting or echo response. Wave species shift their own frequency away from an identical or similar stimulus frequency in a jamming avoidance response.

Evolutionary Considerations

Striking similarities and differences in the structure and functioning of electric organs and electroreceptors, as well as in electric signaling and overt behavior, have evolved *independently* in two unrelated groups of fishes, the South American gymnotoids and the African mormyriforms. We assume today that the presence of a passive electrosensory system, which depends on external electric energy, preceded the evolution of an active electric sense, in which the animal produces its own signal energy. The distribution of ampullary organs in most elasmobranchs and catfish as well as in the weak-electric fishes suggests the possibility of prior stages endowed with a passive electric sense only. Because certain species shifted their preferred habitat to mostly turbid waters and gradually changed to a nocturnal life style, it is plausible that their tuberous electroreceptors — those receptors involved in electrolocation and electrocommunication — evolved at the same time (co-evolution) as the ability to emit weak electric discharges.

It is believed that gymnotoids evolved from ancestors that discharged with variable intervals between discharges, much like the mormyrid pulse species. The selective pressure toward greater mobility necessitated an elongate, hydrodynamic body shape and higher EOD repetition rates to increase the resolution of the electric image. (Another advantage of emitting such higher frequency bands for social communication is their reduced vulnerability in an electrically noisy environment.)

Independently, the African mormyrids evolved electroreceptive and electrogenic structures. Here, the evolution of a noise-resistant communication system has taken quite a different path. Mormyrids evolved a tremendous species-typical diversity in EOD waveforms. The co-evolution of precisely tuned tuberous electroreceptors aids mormyrids in recognizing conspecific, mate-specific, or age class-specific signals in a noisy environment.

Last but not least, the complex communication and orientation systems in weak-electric fishes have certainly not evolved along one single sensory modality, the electric one. Without their electric sense, these fishes are by no means left in the "dark." They have a functional lateral line, respond to chemical stimuli, react to changes in light intensity and temperature, can hear, and have dim-light vision (as was demonstrated for the mormyrid *Gnathonemus petersii*). Thus the fishes' electric organ discharges, serving their dual function of electrolocation and electrocommunication, act in concert with other sensory modalities to aid the fishes in seeking mates, food, and shelter, establishing territories, forming and dispersing social groups, and moving about in their habitats.

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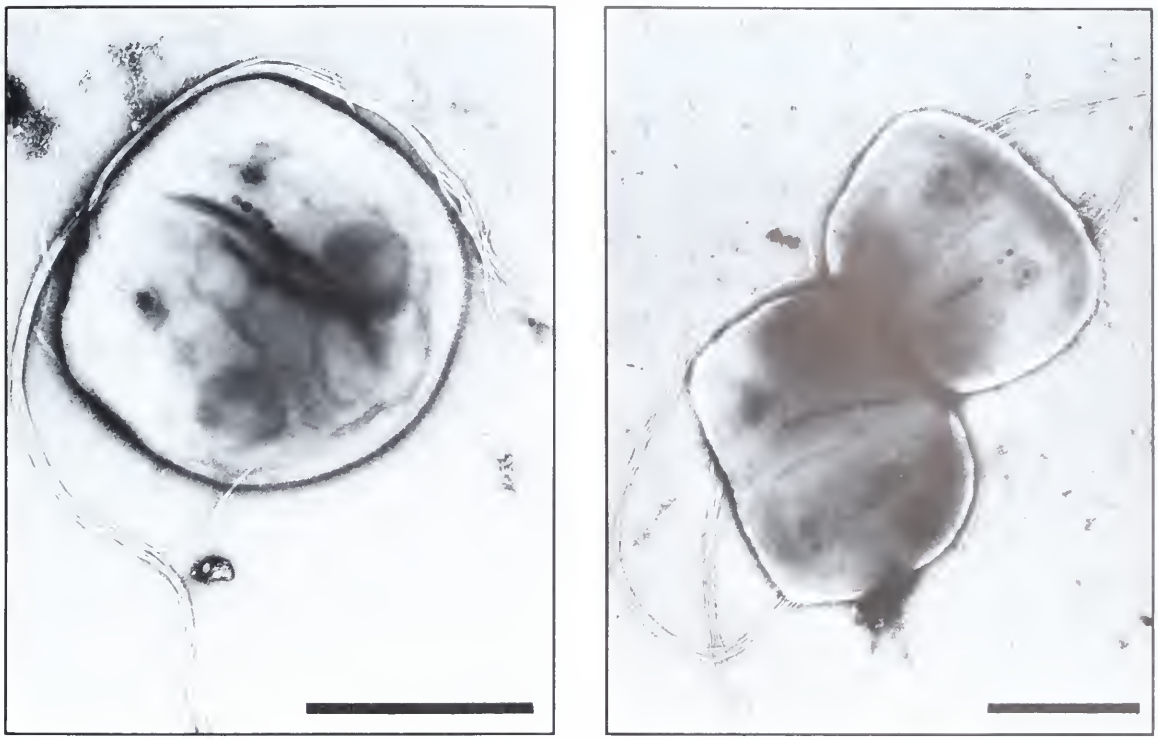

Electron micrographs of freshwater magnetic bacteria from Cedar Swamp, Woods Hole, Massachusetts. Two slender bundles of flagellae mark the posterior ends of the organisms. Note the chains of magnetite crystals and their orientation relative to the cell axis. Calibration bars: 1 micrometer. (Photos courtesy of Richard P. Blakemore)

Geomagnetic Guidance Systems in Bacteria, and Sharks, Skates, and Rays

by Paul R. Ryan

The relatively recent discovery of a magnetic dipole moment — the equivalent of a compass needle — in some sediment bacteria has aroused renewed interest in interdisciplinary studies of animal orientation, navigation, and homing. Although mariners have used magnetic compasses for nearly a thousand years, the finding of ferrimagnetic* orientation in living organisms was made only a few years ago.

In the fall of 1975, Richard P. Blakemore, presently a microbiologist at the University of New Hampshire, reported that certain kinds of marine and freshwater bacteria consistently swam north when separated from the sediments. He found that their direction of swimming could be readily changed by moving a small bar magnet up to the microscope slide.

Blakemore then teamed up with Adrianus J. Kalmijn, a specialist in sensory biophysics at the Woods Hole Oceanographic Institution (WHOI). The two scientists soon established that when the bacteria were tested outside the laboratory — free from man-made distortions of the geomagnetic field — they responded to the earth's uniform magnetic field. In fact, given freedom of motion, the bacteria followed the steeply inclined field lines, rapidly returning to the bottom substrate at an angle of about 70 degrees.

The tendency of the bacteria to swim north was especially evident when the ambient magnetic

*A form of natural magnetism occurring in magnetite and other minerals.

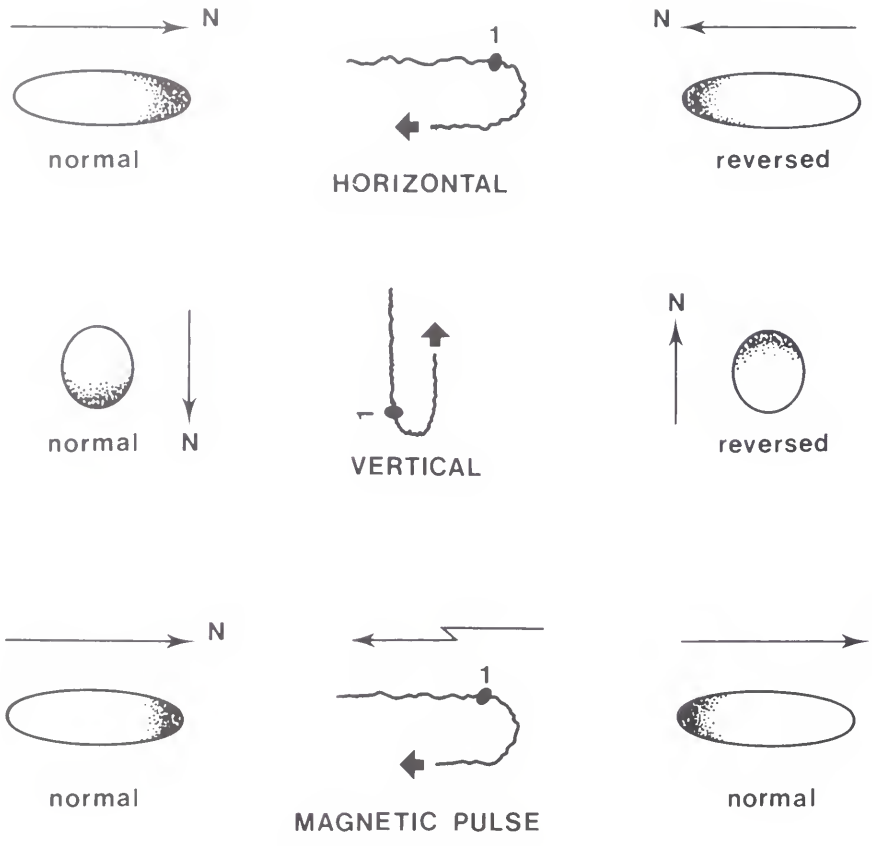

Figure 1. Top line: bacteria collecting along the north side of a water droplet. Reversal of the horizontal component of the earth's magnetic field (at dot along track) makes them migrate to the opposite side of their small puddle. Middle line: similar results are obtained in the vertical plane, despite gravity. Bottom line: a strong magnetic pulse of short duration, applied antiparallel to a steady background field, causes the bacteria to turn around and swim south, resulting from the reversal of their intrinsic biomagnetic dipole moment. (After Kalmijn and Blakemore, 1978)

field was reversed with the aid of Helmholtz coils*: under the microscope, the organisms immediately changed course, making 180-degree U-turns several cell diameters wide. They realigned themselves with the field in a matter of seconds, this time heading in the opposite direction.

Observations on the behavior of these bacteria with regard to magnetic fields led to the conclusion that they have a permanent magnetic dipole moment. A magnetic dipole has a north pole at one end and a south pole at the other. The strength of the poles, multiplied by the distance between them, is the dipole moment. In short, a bacterium has a miniature built-in bar magnet and consequently the whole organism, when freely swimming, acts as a compass needle.

Each cell contains chains of electron-dense crystals parallel to its axis of motility. Richard B. Frankel, at the Massachusetts Institute of Technology's Francis Bitter National Magnet Laboratory, determined that these crystals consist mainly of magnetite, a strongly magnetic iron compound. When cultured in iron-deficient media, the organisms often lose these crystals, in which case they no longer respond to imposed magnetic fields.

When the cells are separated from the mud, the magnetic bacteria are affected by the directive force of geomagnetic field alignment and the randomizing effect of thermal agitation (Brownian motion*). They therefore resemble the passive dipole particles in French physicist Paul Langevin's theory of magnetization. Although passively orienting along field lines, the Woods Hole species actually propel themselves in a northerly direction by flagellar action. (In the Southern Hemisphere, the bacteria swim in a southerly direction, thereby reaching the bottom substrate again.) Studies have shown that the dipole moments largely overcome the effects of Brownian motion and of swimming irregularities. In the experiments, the bacteria do not appear to be noticeably affected by the force of gravity in their downward descent (Figure 1).

*A pair of Helmholtz coils is the simplest means of generating a sizable uniform magnetic field.

*The increasing and irregular motion of small particles, such as pollen grains, when held in suspension in a liquid. It is a visible demonstration of molecular bombardment by the molecules of the liquid. The smaller the suspended particles, the more noticeable the motion.

How the Work Was Done

The freshwater and marine magnetic bacteria were collected from Cedar Swamp and Eel Pond in Woods Hole, Massachusetts. The mud samples were taken from the top layer of the sediments and were kept in glass jars under laboratory conditions.

Kalmijn's ongoing studies present a quantitative description of the bacteria's migratory behavior resulting from passive magnetic field alignment and flagellar motion. The bacteria selected have their flagallae at one end and propel themselves in one direction, swimming steadily when separated from the sediments (Figure 2).

The testing site at Woods Hole is located in a basement where the earth's magnetic field is fairly undistorted. Two pairs of Helmholtz coils null the earth's magnetic field, while two more pairs produce a horizontal test field of either normal or reversed polarity. The field strength is selected from seven pre-calibrated settings, ranging from slightly above to slightly below earth's magnetic intensity. The bacteria are observed under a Zeiss surgical microscope at a magnification of 83.2 x and are illuminated obliquely against a dark background.

The first step in measuring migration rates is to transfer one or a few bacteria from the sediments into a small observation chamber built upon a standard hemacytometer slide (normally used for blood counts). In the chamber, microanaerobic conditions are maintained because exposure to oxygen would cause the bacteria to slow down. A graticule (scale) etched in the bottom of the chamber provides a calibrated grid with major divisions 1 millimeter apart.

The migration rate of a single bacterium is determined by recording the time of travel in the direction of the field over the measured 1-millimeter distance. After each test, the magnetic field is reversed to make the bacterium traverse the same distance in the opposite direction. Single cells have been observed swimming back and forth more than a hundred times without noticeably slowing down, but a point is finally reached when there is a dramatic drop in motion, perhaps because of exhaustion.

Thus far, the migration rates of 16 freshwater bacteria have been recorded, the first six of which

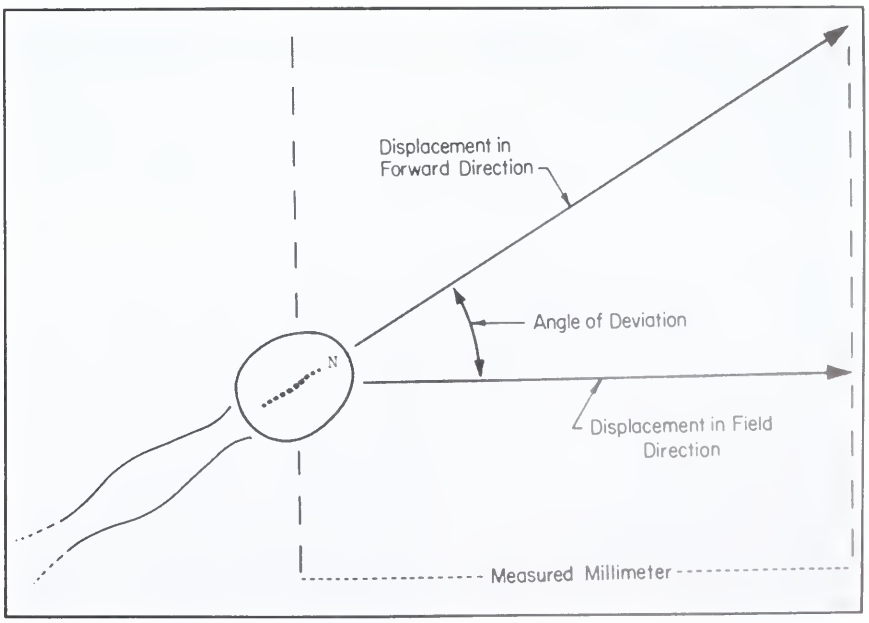

Figure 2. The functional relationship between the average rate of migration and the amount of swerving in magnetically orienting bacteria. In a magnetic field, the average cosine of the angle of deviation equals the time of travel along the measured millimeter at high field strength (without swerving) divided by the time of travel at field strength under consideration (with swerving). With increasing field strength, the speed of travel (in the direction of the field) approaches the speed of swimming (along the axis of motility). Note the chain of magnetite crystals oriented to align the bacterium with the magnetic field direction. N is north pole. Bacterium not to scale. (From Kalmijn, 1980)

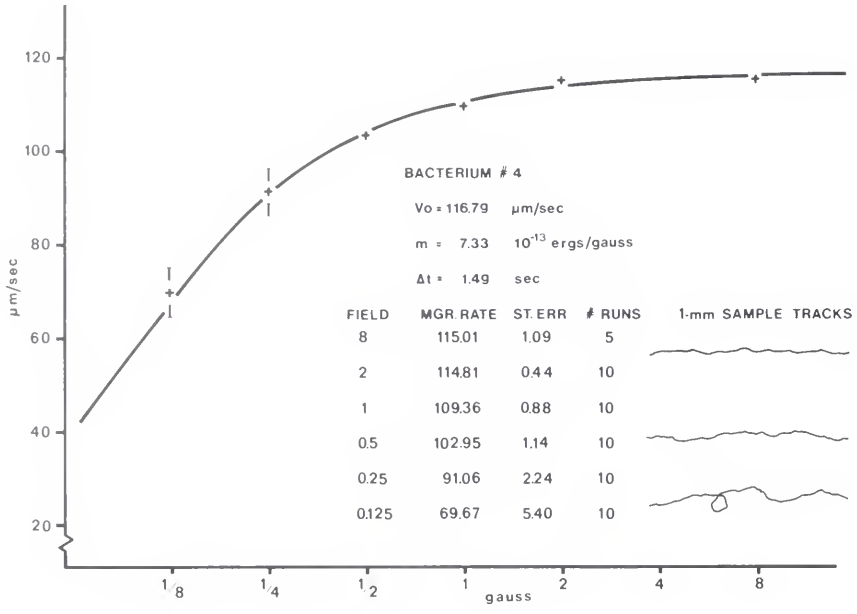

Figure 3. In magnetic bacteria, the dipole moments of single cells and the efficacy of the orientation mechanism are determined from the rates of migration along magnetic field lines. Plotted are the rates of migration as a function of ambient field strength. Vo is the speed of swimming along the axis of motility; m is the magnetic dipole moment of the cell. At the earth's magnetic field strength, this bacterium migrated at a rate of 88 percent of its swimming speed, losing only 12 percent to the randomizing effect of thermal agitation and swimming irregularities. (After Kalmijn, 1980)

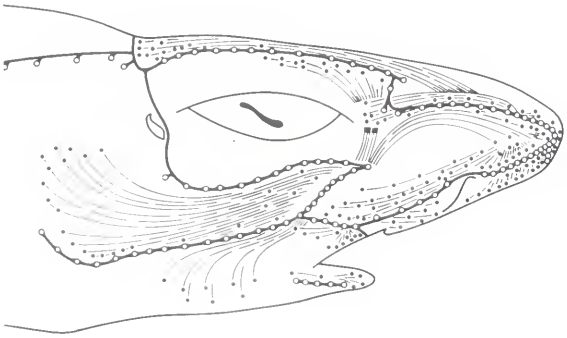

Figure 4. Ampullae of Lorenzini and mechanical lateral-line system in head region of the shark Scyliorhinus canicula. *Solid dots: skin pores of electroreceptors. Small circles: openings of lateral-line canals. (After Dijkgraaf and Kalmijn, 1963)*

have been fully analyzed. One of these tests is summarized in Figure 3.

From these results and from the amount of magnetite seen in electron micrographs, the scientists have determined the dipole moments of individual bacteria. These dipole moments appear to be well adapted to orientation in the earth's magnetic field. The bacteria migrate at speeds that amount to 80 to 90 percent of their forward thrust. Swimming at speeds of more than 100 micrometers per second, these tiny travelers may run a distance of 36 centimeters within an hour.

Related Work

Kalmijn and student collaborators at WHOI have found that sharks, skates, and rays — commonly referred to as elasmobranch fishes — are extremely sensitive to weak electric fields in their seawater environment* (see *Oceanus*, Vol. 20, No. 3, p. 45; also see page 48, this issue). These low-level electric fields are detected by the ampullae of Lorenzini — a delicate sensory system in the protruding snout of elasmobranch fishes (Figure 4). In recent years, the ampullary receptors of both marine and freshwater electrosensitive fishes have been shown to play an important role in the detection of prey and in spatial orientation.

All aquatic animals produce weak DC and low-frequency electric fields, which stem from potential differences at their skin/water interfaces. Marine sharks, skates, and rays take advantage of

*Elasmobranchs show biologically meaningful responses to voltage gradients as low as 0.005 microvolts per centimeter.

these bioelectric fields in predation. When motivated by odor, they zero in on their prey even if it is a small animal hiding in the sand, such as a flounder. These observations, originally made under well-controlled laboratory conditions, were later verified in the field on free-roaming sharks in the ocean off Cape Cod and on wild catfish in a Woods Hole freshwater pond.

Wind-driven and tidal ocean currents flowing through the earth's magnetic field induce electric fields that are perpendicular to and, in the Northern Hemisphere, directed to the left with respect to the flow of water. When measured with towed electrodes, the induced voltage gradients range from 0.05 to 0.5 microvolts per centimeter. In these fields, marine elasmobranchs may orient electrically, either to compensate for passive drift or to follow the ocean currents during migration. In freshwater, the prevailing electric fields are much stronger and of electrochemical rather than electromagnetic origin, offering more local, territorial cues.

When actively swimming through the earth's magnetic field, sharks, skates, and rays also induce local electric fields of which the voltage gradients depend on the fishes' compass heading. As these fields are strong enough to be detected at swimming speeds of only a few centimeters per second, the elasmobranchs could very well be endowed with an electromagnetic compass sense.

In behavioral experiments, the animals indeed have demonstrated their ability to orient to uniform electric fields such as those which appear in nature (Figure 5). In similar tests, it has been shown that they also have the ability to orient to the earth's magnetic field (Figure 6).

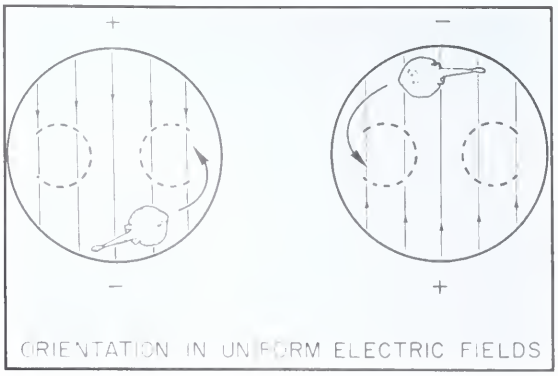

Figure 5. To receive reward and to avoid punishment, the stingray Urolophus halleri *enters the enclosure to the right, avoiding the one to the left with respect to the field. Accordingly, after reversal of the field, the animal again seeks food in the enclosure to the right with respect to the field, though it is now located at the opposite side of the tank.*

Some History

The mysterious power of lodestone to attract iron was known to the ancient Chinese and Greek civilizations. The Greek name for lodestone — *magnes lithos* or stone from Magnesia — probably derives from its place of origin in Asia Minor. However, not until the millennium AD was it recorded that an iron needle, magnetized by stroking it with lodestone, points north when made to rotate freely. This discovery gradually led to the construction of magnetic compasses, which enabled mariners to orient at sea more confidently.

It was subsequently noticed that in the Northern Hemisphere the compass not only

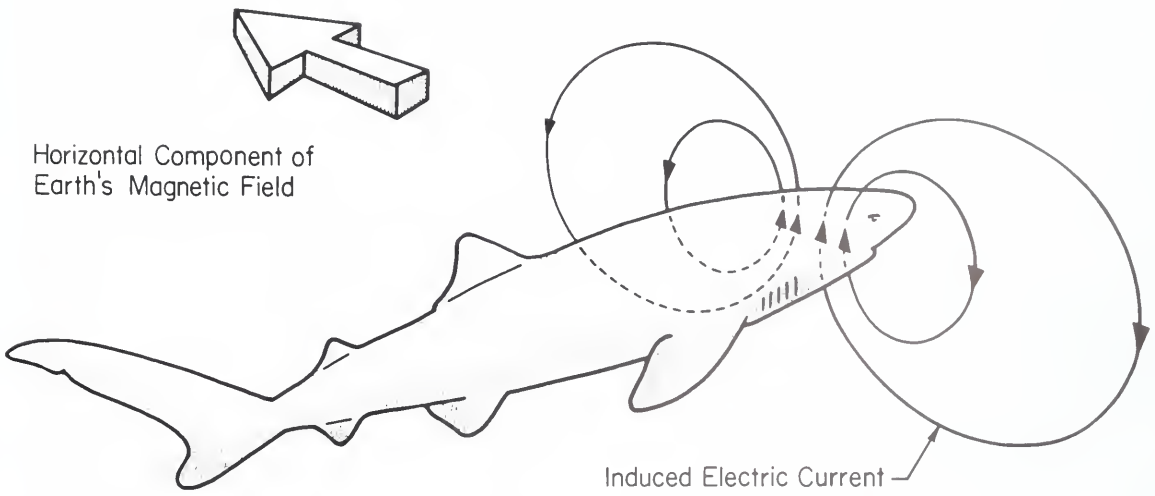

Figure 6. A shark swimming through the earth's magnetic field induces electric fields giving the animal's compass heading. (From Kalmijn, 1974)

oriented North, but also inclined downward, indicating that the directive force was of terrestrial rather than celestial origin. William Gilbert (1600), in his treatise "De Magnete," observed that the earth's globe itself is endowed with a magnetic field similar to that of a lodestone sphere.

Realizing that the need for orientational cues is not unique to human travelers, natural scientists have often wondered whether animals, in particular migrating birds, might not direct themselves by the earth's magnetic field as well. In the last few decades, affirmative evidence has been obtained, especially from studies on migratory birds, homing pigeons, elasmobranch fishes, and sediment bacteria. From this work, the two detection mechanisms emerged, one based on the principle of electromagnetic induction (in elasmobranchs), the other on permanent magnetic dipole alignment (in sediment bacteria).

The Road Ahead

Experiments have left little doubt that elasmobranchs sense the earth's magnetic field and may direct themselves accordingly, whereas magnetic bacteria are committed to swimming along field lines by passive dipole alignment. The orientation of magnetic bacteria is largely determined by physical forces. In the sediments, other factors also control their behavior. Thus the elasmobranchs' compass orientation and the bacteria's magnetically directed migration suggest an important role for their "magnetic sense" in daily life. However, adequate field studies will be required to verify such a plausible, yet conjectural conclusion. Thus the discovery of a biomagnetic compass has implications far beyond the microbial level, signifying a possible major breakthrough in the study of animal orientation, navigation, and homing.

Paul R. Ryan is Managing Editor of Oceanus, *published by the Woods Hole Oceanographic Institution.*

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The author would like to acknowledge the help and advice given in the preparation of this article by Adrianus J. Kalmijn, a specialist in sensory biophysics at the Woods Hole Oceanographic Institution. In addition to granting this author interviews as well as providing laboratory demonstrations of bacteria migration, Kalmijn offered guidance on what path to take through the literature on the subject. Others who were helpful include Richard P. Blakemore of the Department of Microbiology, University of New Hampshire, and Richard B. Frankel of the Francis Bitter National Magnet Laboratory at the Massachusetts Institute of Technology.

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RIPPLE COMMUNICATION

by R. Stimson Wilcox

On the surface of a small pool, a blue sky lies quietly reflected, intermingled with golden-shaded rocks on the bottom (Figure 1). Occasionally the reflection undulates with passing surface ripples produced by insects swimming on the surface, then the ripples pass on and the sky returns to undisturbed reflection. The elastic surface of water is thus the home of beautiful reflections, as well as of many organisms that live both atop and underneath the surface film. Of particular interest is the role the water surface plays in the biology of surface-dwelling insects called water striders (family Gerridae). These insects use the water surface as a mode of communication by making ripple signals while they swim about.

Surface-Dwelling Animals

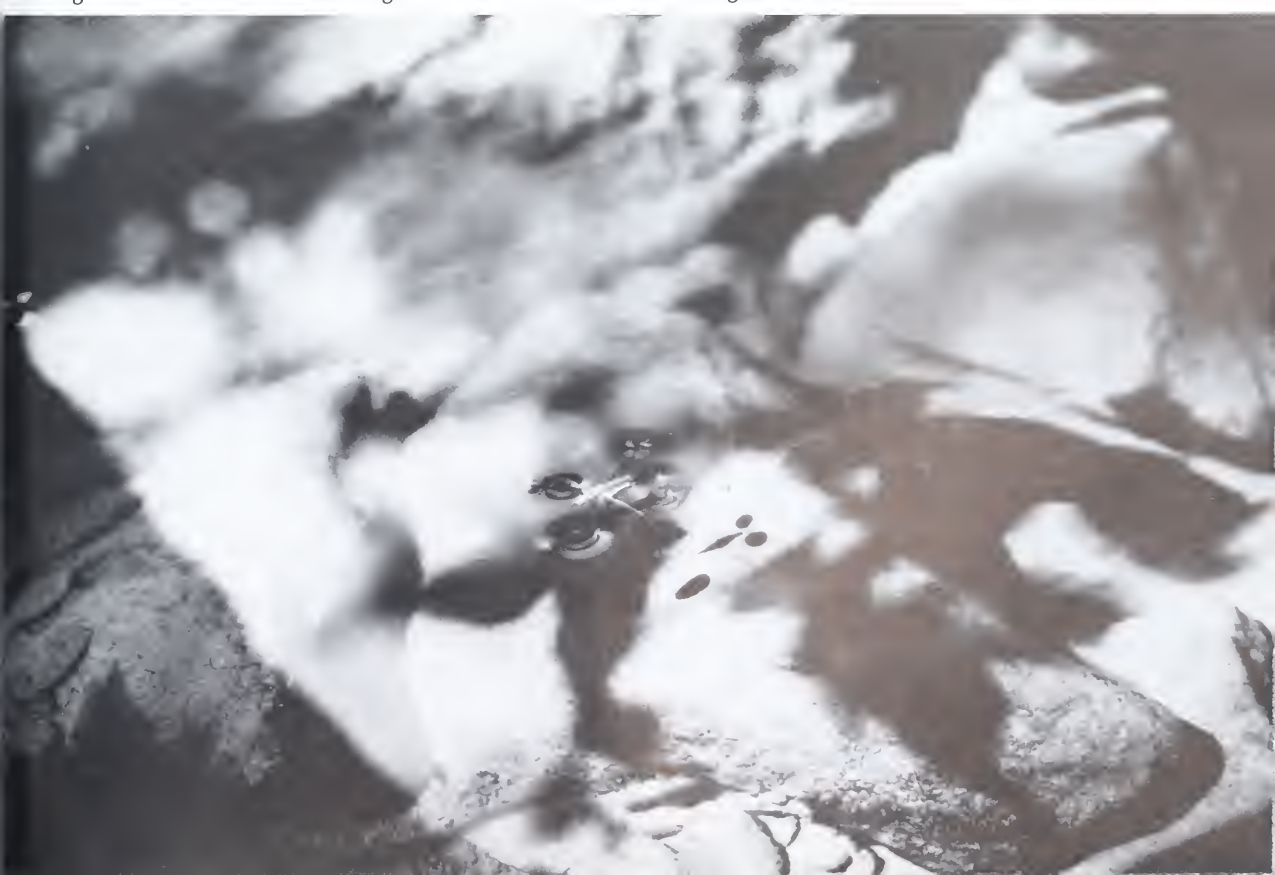
Many animal groups use the surface of freshwater as a substrate. Those which utilize mainly the top of the surface include at least four other families of Hemiptera besides water striders, and a few species of beetles (especially Gyrinidae, the whirligigs), spiders, flies, and springtails. Species that use the surface mainly from below include backswimmers (Notonectidae) and a few species of at least four fish families.

In the marine environment, three groups of insects use the surface: several species of the water strider genus *Halobates*, which are the only insect species that inhabit the open oceans; another hemipteran of the genus *Halovelia*; and marine springtails. Of course, many other marine animals live at the surface film, such as floating snails and jellyfish.

Why Live at the Surface?

Animals have good reasons for using the surface film as a substrate. The asymmetry of attractive forces on water molecules at the surface results in these molecules forming an elastic membrane that

Figure 1. Water strider Gerris remigis *in the center of a stream near Binghamton, New York.*



can support considerable weight. For example, most of us are familiar with a needle floating on the surface of a cup of tea. Photographic studies show that when water striders are swimming, the surface film actually folds down and back on itself without rupturing, giving the leg of the organism a good purchase. Other surface-dwelling insects, of the family Veliidae (similar to water striders), not only swim on the surface, but also release a salivary secretion that lowers the surface tension in a rapidly spreading circle. They catch a quick ride on the edge of the spreading circle, and in this way move much faster than usual.

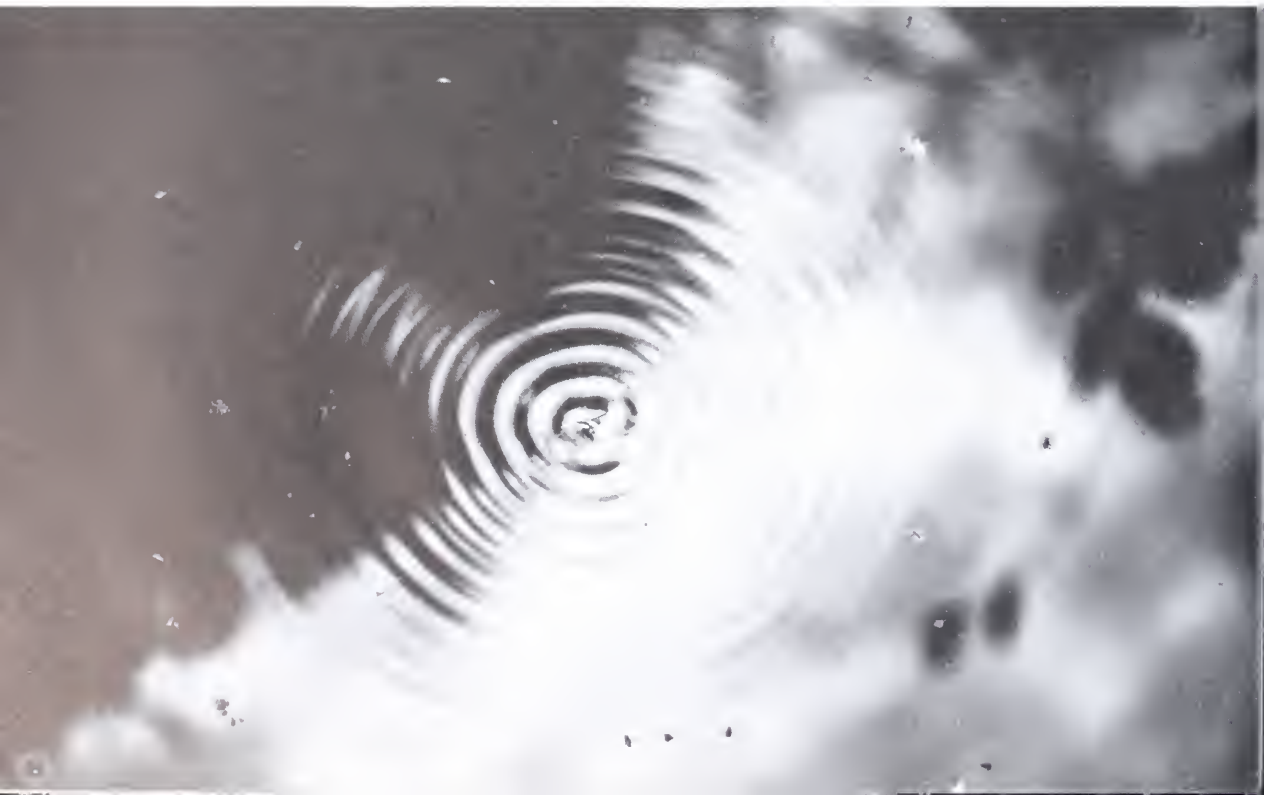
For small organisms not adapted to moving about on it, however, the elasticity of the surface forms a deadly clinging trap, resulting in an ideal two-dimensional surface for predators to roam about on in search of prey. In fact, it is probably because of the concentration of prey in the surface film that the majority of surface-dwelling organisms evolved as specialists, not to mention the surface-feeding behavior of flying birds, bats, and insects from above, and insects and fishes from below. The result of such prey exploitation is often intense competition for food in the surface film.

Surfaces and Surface Waves

Any disturbance of the water surface causes the generation of surface waves, which emanate out in concentric circles. Such waves are basically similar to the pressure waves involved in transmission of acoustic or compressional waves, involving the periodic, back-and-forth movement of molecules (see *Oceanus*, Vol. 20, No. 2). Surface (Rayleigh) waves differ, however, in that they have a vertical component as well as horizontal components, and they travel slower. Surface waves occur in solids and liquids, which have definitive surfaces.

It has long been known that animals orient toward surface waves, especially toward surface-wave-generating prey, such as spiders, which locate prey in their webs; scorpions, which locate nearby prey on land; and fishes, gyrinid beetles, backswimmers, and water striders, which find prey in the surface film. According to the usual definition of communication — in which signals and receptor capacities have been shaped by natural selection for communicating and receiving particular messages, or for manipulating the receiving organism — the activity of predation on prey is not considered to be communication. However, substrate communication among members of the same species (intraspecific communication) is now known to exist in many invertebrates and vertebrates. Although it generally has been assumed that substrate signals are transmitted by acoustic vibrations, it is probable that surface waves are a partial or major component of the signals involved. There has not been any

Figure 2. A calling signal being produced by a male water strider Rhagadotarsus kraepelini *on a pond near Cairns, Queensland, Australia. The organism's body is the oval white dot at the pattern's center. The strider is grasping a small piece of floating wood (a signal site) while producing the signal.*



doubt about surface wave involvement in the case of the spider.

Surface wave or ripple communication in water is the most recently discovered mode of intraspecific communication. So far, the literature has described this type of communication in only a few species of water striders.

Ripple Communication in Water Striders

There are several ways in which animal signals of any communicative mode (for example, visual and chemical) appear to be patterned or coded: in signal frequency, timing, intensity, content, and combinations thereof, not to mention combinations of different sensory modes. Most animal species, water striders included, exhibit the full range of patterning ploys.

Figure 2 shows a ripple signal being produced by a male *Rhagadotarsus kraepelini*, a species distributed in tropical areas from India to eastern Australia. *Rhagadotarsus* inhabits ponds or slow-flowing eddies along streams. Adult males of this species produce ripple signals for precopulatory calling and courtship, copulation, postcopulation, individual spacing, and territoriality (Figure 3). All striders studied to date

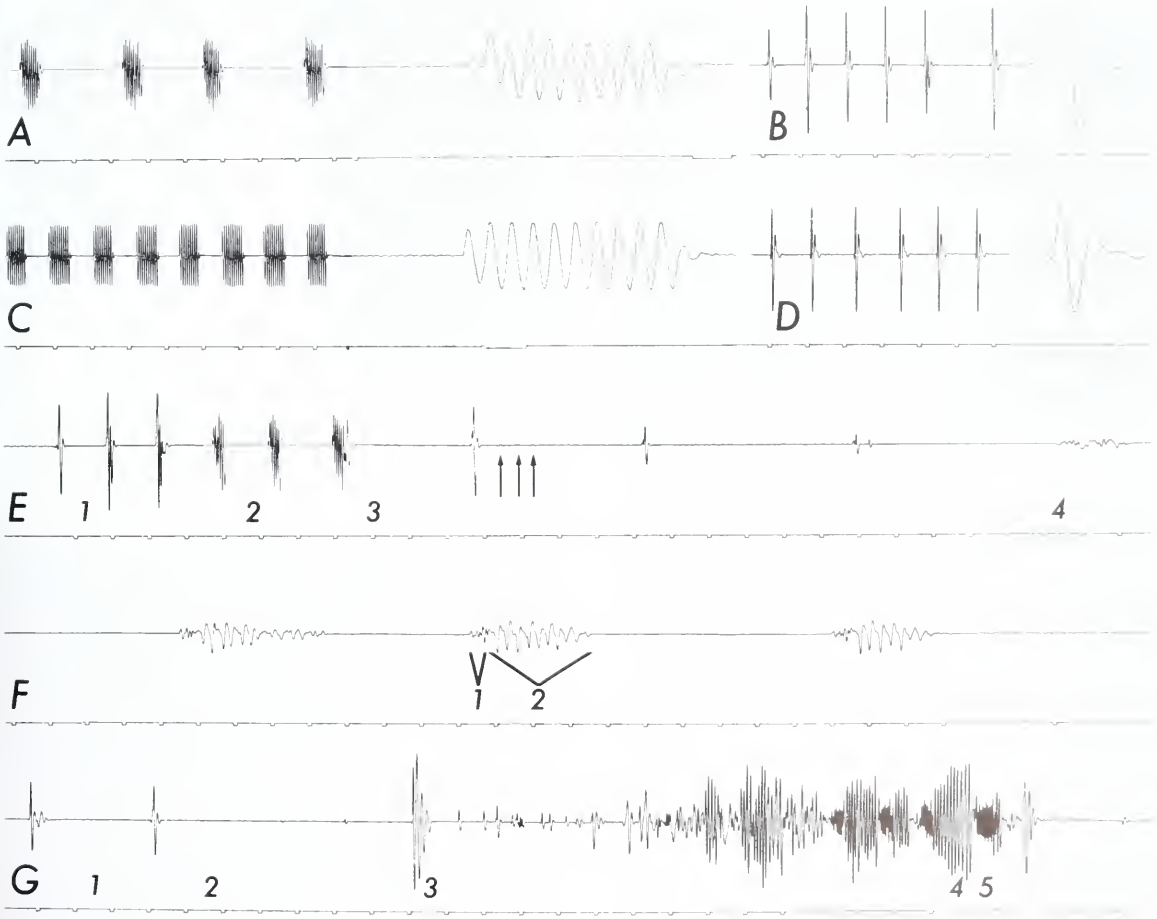


Figure 3. (A) Calling signals of male Rhagadotarsus. *Central portion of each signal is approximately 18.5 waves per second. One signal expanded ten times (right); similar expansions in B, C, and D. (B) Courtship-calling signals. (C) Artificial calling signals (17.5 waves per second). (D) Artificial courtship-calling signals. (E) At 1, male begins signaling with courtship-calling signals, increasing the number of waves to calling signals at 2; at 3, a female approaches within 5-10 centimeters of male, who changes to courtship (for example, three arrows — barely discernible blips) and courtship-calling signals; between 3 and 4, a female approaches within 2-3 centimeters; and at 4, a female grasps and pulls the male's leg, causing movements of float. (F) Male copulatory signals. (G) At 1, a male produces courtship-calling signals; at 2, another male approaches closely; at 3, the first male produces an aggressive signal, but the second male grasps the float also. A dispute follows, with both males grasping the float. At 4, there is a lower frequency (9-13 waves per second) signal; and at 5, a higher frequency (23-30 waves per second) signal. All time markers at 1-second intervals. A, B, C, and D (right) recorded at a chart speed of 20 centimeters per second; all other signals recorded at 2 centimeters per second. (From Wilcox, 1972)*

produce signals by simultaneous vertical oscillations of one pair of legs, or up to all three pairs of legs, sometimes with distinct vertical body motion also. *Rhagadotarsus* is unique among the striders in that it uses a physical site, such as a floating or fixed piece of twig, to signal from. It also exhibits lekking behavior, where several males, defending territories around signal sites, vie for attention of sexually receptive, choosy females. This behavior is similar to the lekking known in a few other species of insects and in many fishes, birds, and mammals. In *Rhagadotarsus*, territoriality around signal sites may have evolved because the female lays an egg in a signal site following each copulation; thus it behooves males to defend good signal sites.

Studies using a site to generate signals have shown that calling signals alone (played back at 22 waves per second) will induce a female *Rhagadotarsus* to approach, grasp, and lay eggs in the site, with no male present. Females not only are internally tuned to the calling signal frequency, but also can discriminate between signals whose frequencies are only 1.5 waves per second apart. Also, the entire mating and egg-laying sequence can occur in total darkness. This raises the question of the extent to which vision is used during mating behavior in this species. It also provides another example of how some communicative modes may be decreasing in use while others are evolving toward greater usage.

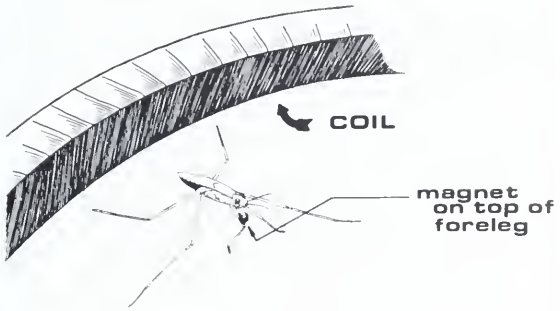
Another function of a ripple signal has been demonstrated in *Gerris remigis*, a large and common water strider that inhabits small North American streams. Adult males of this species produce high-frequency (HF) ripple signals of around 85-90 waves per second (Figure 4), mainly in spacing behavior (including territoriality and food defense). Recent studies have shown that males can use the presence or absence of HF signals to discriminate between sexes — since only males produce them. In our experiments, females were made to artificially produce HF signals. This was done by gluing a tiny but powerful magnet onto the foreleg of a female, then allowing her to swim freely inside a coil of magnet wire (Figures 5 and 6). Amorous males blinded with form-fitting rubber masks invariably tried to mate with females that did not produce artificial HF signals, and did not try to mate when the signals were played back. Since males were blinded, and sometimes were in body contact when they rejected HF signal-producing females (eliminating chemical and visual cues), they appear to be able to discriminate between sexes solely by the presence or absence of HF signals.

Ripple Signal Characteristics

To be effective, ripple signals must be distinctively nonrandom, characteristic of a particular species, and capable of transmitting a signal over a sufficient distance. The nonrandomness of simple repetition signals — such as the calling signal of *Rhagadotarsus* (Figure 3A) or the HF signal of *G. remigis* (Figures 4 and 6) — is enough of a cue to a ripple signal receiver, which also records the number of ripples per signal, signal intervals, and particular frequencies, intensities, waveforms, and contexts. The more obvious intraspecific functions of signals, such as involvement in sexual identification and stimulation, reproductive isolation, and spacing behavior, may be added to by a less obvious function — recognition of conspecifics.

Figure 4. A high-frequency (HF) ripple signal produced by a male water strider Gerris remigis *on a stream near Binghamton, New York. The signal is produced as part of an aggressive encounter between a territorial male and an intruder.*

One of the major sources of mortality in water is cannibalism. Well-fed water striders do not usually eat their own young, but hungry ones apparently eat anything that moves. Species-distinctive ripple signals may inhibit the predatory tendencies of hungry striders, given that the signals are generally produced by individuals whom it would be difficult or impossible to subdue. Horst Lang of the University of Karstanz, West Germany, has shown that *Notonecta* (a backswimmer) is capable of recognizing the differences between waves made by its own species



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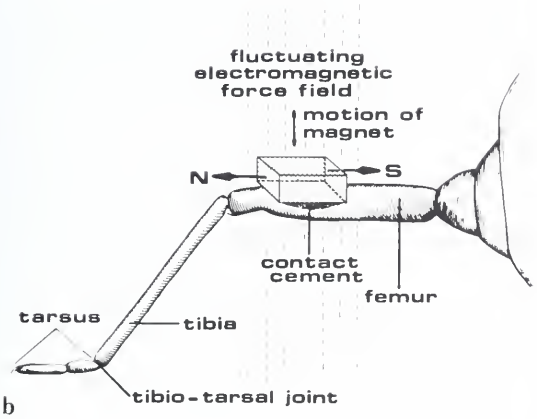

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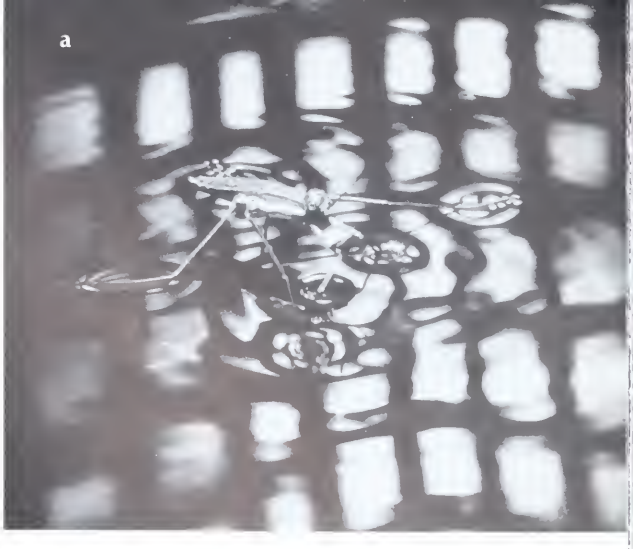
Figure 5. (a) A female Gerris remigis *producing a computer-generated ripple signal (the HF signal, normally produced only by males). The signal is produced by the movement of a tiny magnet glued on top of the female's foreleg. The horizontal coil of magnet wire generates a fluctuating electromagnetic field when fed an analog signal from the computer. (b) Closeup showing the exact placement and orientation of the magnet. A microcomputer was used to digitize, analyze, store, retrieve, and generate the playback signal through an amplifier into the coil. The electromagnetic fluctuations made by the coil oscillated the magnet, making the female's leg produce a (male) HF ripple signal each time a button was pressed.*

during nymphal and adult stages, and also the waves produced by some prey species. The greater distinctiveness of signals in water striders would make such conspecific-versus-prey species recognition that much easier.

It is well known that over distance, high-frequency vibratory signals are dampened quicker than low ones. In general, long-range signals have been shown to contain more energy in lower frequencies, and short-range signals include higher frequencies. On water, waves of 1 micrometer amplitude and of 80 waves per second frequency dampen out almost entirely after traveling a distance of only about 9-10 centimeters.



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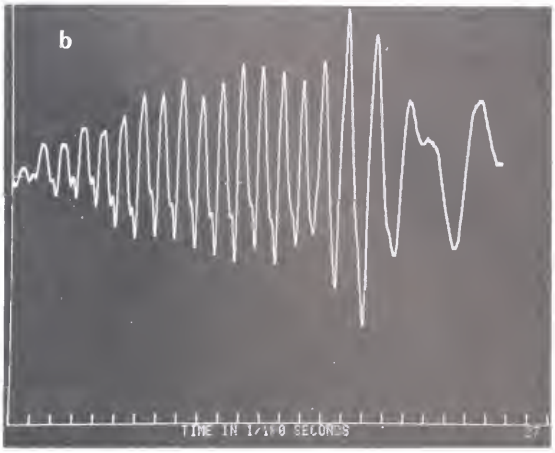

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Figure 6. (a) A female Gerris remigis *producing a computer-generated male HF signal by the coil-and-magnet technique. The female is also blinded by a form-fitting mask of opaque silicone rubber. (b) The HF ripple signal in profile. The frequency of this signal averages 90.4 waves per second.*

The calling signal of *Rhagadotarsus*, with a range of at least 40-60 centimeters, is about 22 waves per second, whereas the short-range, highly repetitive signal of *G. remigis*, which is not used at distances greater than about 9-10 centimeters, is about 85-90 waves per second. Other signal characteristics, such as divergence in features for species identification, are thus constrained by physical and biophysical factors — frequency damping, oscillatory rates of neurons, signal-producing legs, and so on.

One of the main advantages of ripple signal communication, as in vibratory, contact, electrical, thermal, and chemical communication, is that it can take place in the dark or in areas where vision is limited. The degree to which ripple signals and visual signals (or other types of signals) interact in water striders has not yet been investigated. Hedi Meyer, of the University of Frankfurt, West Germany, has found that *Velia*, a surface dweller

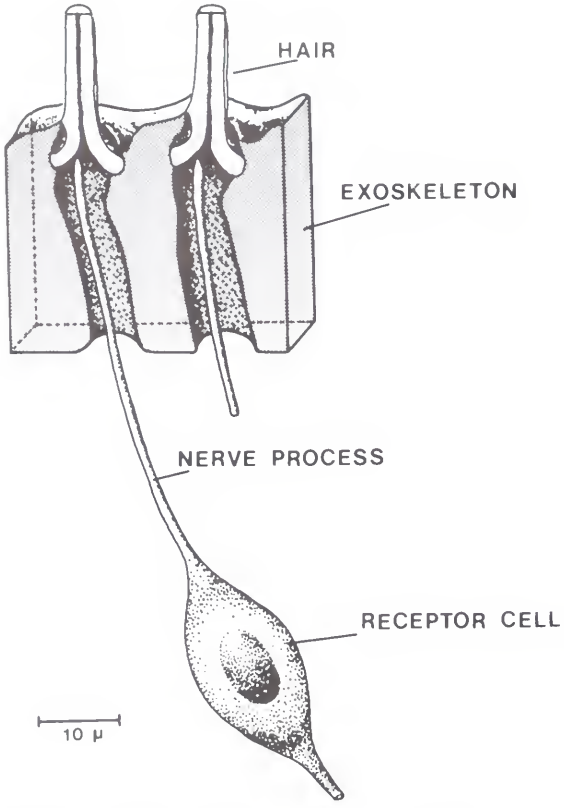

Figure 7. An insect mechanoreceptor, one of many variations. Shown is part of the hair-plate organ in the neck of a bee. The distal nerve process of a bipolar receptor cell enters the joint region of a hair through a canal in the cuticle. Each stiff hair is roughly 100 micrometers long. The receptor cell generates nerve impulses as a result of the movement of the hair in its socket.

related to the water strider, will not respond to visual cues unless a simultaneous artificial surface wave pattern is also presented.

Sensing and Orienting to Ripple Signals

Most arthropods sense substrate vibration by one or both of two ways: distortions in the exoskeleton, caused by vibrations, are sensed by stretch receptors; and movements of sensory hairs that are seated in flexible sockets excite impulses in nerve cells at the hair bases (Figure 7). Variations of such receptors are involved in vibration reception in all arthropod groups, as well as in sound reception in many species. The exoskeleton stretch receptors are part of the overall proprioceptive system (where stimuli arise within the organism), whereas the sensory hairs are concerned with external stimuli. However, at low frequencies, the two systems overlap considerably.

Although there have been no studies of the mechanisms involved in ripple signal reception, work has been done on surface wave reception in the amplitudes and frequencies produced by prey struggling in the surface film. Studies on *G. remigis* by Rod Murphey, of the State University of New York at Albany, indicate the presence of stretch receptors in the strider's tibio-tarsal joint (Figure 5b). The strider responded to low-amplitude surface waves (5 micrometers at 20-30 Hertz) when the tarsal segment but not the joint was clipped off, but did not respond if the tarsal segment plus the joint was clipped off. However, a competing theory on the existence of a stretch receptor in the tibio-tarsal joint has been presented by J.V. Lawry, then at the University of California, San Francisco. He suggests that long, omnidirectionally-socketed hairs on the tarsal segment of the leg are used for sensing surface waves. This situation is still unresolved; perhaps future work will show that both mechanisms are involved. Indeed, *Notonecta glauca* (a backswimmer), uses sensory hairs in addition to leg joint stretch receptors to sense surface waves.

Another surface-dwelling group that has been studied for surface wave reception is whirligig beetles. Whirligigs mainly use a joint stretch receptor system called the Johnston's organ, which senses surface wave-induced motion between two segments of the antennae lying flat on the water surface. The mechanoreceptive systems involved in surface wave reception are very similar to terrestrial mechanoreception — for example, spiders sense waves on their webs and scorpions sense waves in the surface of sand in much the same way as water surface dwellers.

Regardless of how surface waves are sensed, the mechanoreceptors are remarkably sensitive. Figure 8 shows a water strider responding to a wave

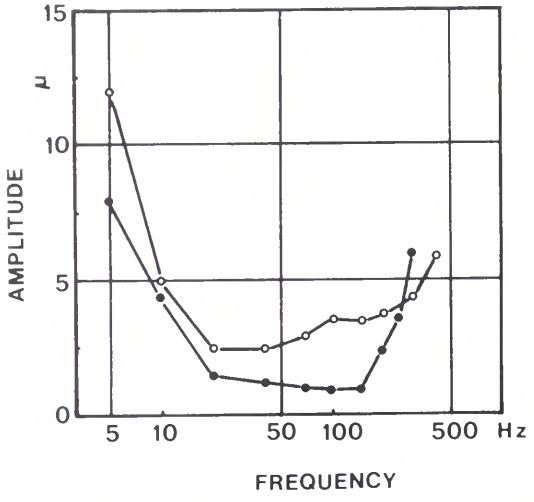

Figure 8. Frequency response characteristics of the surface wave sensors of the water strider Gerris lacustris *(○) and the backswimmer* Notonecta glauca *(●), as a function of surface wave amplitude.*

amplitude of 2.5 micrometers, between 20 and 40 Hertz, and a backswimmer sensing amplitudes of as little as 1 micrometer, between 100 and 150 Hertz. (Animals respond differentially to the same amplitude or intensity of a vibration signal, depending on the frequency or pitch of the signal. It is much easier for humans to hear a 2,000-Hertz tone at a given intensity than it is to hear a 12,000-Hertz tone at the same intensity.) The world of a water strider is enriched by its ability to sense and filter out a near-continuous kaleidoscope of surface wave impressions.

Water striders also are extremely sensitive to pressure waves from below. It is almost impossible for a surface-feeding fish to catch an adult water strider, if the fish does not have a mouth large enough to suck the strider down with a large gulp. One wonders about the capacity of surface dwellers to sense earthquake tremors. And imagine the possibility of the open-ocean-going *Halobates* water strider sensing the passage of submarines by subsurface pressure waves, much less sensing it when the water surface is quiet. The collapse of the wake of a submerged submarine causes capillary waves (waves of a wavelength shorter than 1.73 centimeters) to form on the surface. The only other ways capillary waves can form on the surface are by other animals or falling objects, including crashing waves, since capillary waves are too short in wavelength to be formed by wind, no matter what its velocity. What a spy system the 39 known species of *Halobates* might have!

Orientation to Surface Waves

Surface dwellers are quite accurate in their ability to locate a source that is generating surface waves. Studies on water striders and backswimmers have shown that orientation can occur by the animal's sensing the comparative time of arrival of a wave as it hits in sequence the first two legs. From this comparison, the animals apparently compute the appropriate vector and orient as they move. There is also some evidence from Murphey's work on *G. remigis* that single leg receptors have directional sensitivity. The directional sense certainly works well; for example, when approaching a calling male, a female *Rhagadotarsus* usually swims in a direct beeline (striderline?) toward the male, from as much as 40 to 60 centimeters away.

Other Modes of Communication in Water Striders

In addition to using ripple signals, striders communicate by visual and tactile cues. For example, they visually repel advances by, or nearness of, others by lifting the leg nearest the intruder and also by "stilting up" high on their legs, sometimes so high that the forelegs do not even touch the surface. They may also use these actions to deter a strider that is touching or grasping them. Other examples of tactile cues include males of some species "antennating" females, and rapidly shaking them, immediately preceding and during copulation.

There is no evidence yet of chemical communication in water striders. There is evidence, however, that whirligig beetles repel fishes by releasing a distasteful chemical substance called gyrinol. As for sound, a species of the hemipteran family Veliidae (related to water striders) supposedly has sound-producing structures, although apparently no one has studied it. None of the ripple-signal-producing striders has yet been found to communicate acoustically.

Evolution of Ripple Communication

Ripple signals are used in most communication exhibited by arthropods — species recognition, mating, and spacing behavior. There is no evidence specifically pointing to individual recognition, but this may well occur in some species. All six species of *Gerris* examined have this signaling system, producing signals with frequencies ranging from 3-5 waves per second to 85-90 waves per second. However, except for *Rhagadotarsus kraepelini*, a cursory examination of some species in a few other gerrid genera (such as *Rheumatobates* and *Trepobates*) and of a few non-gerrid genera (for example, *Velia* and *Mesovelia*) has not yet revealed obvious ripple signal systems.

When you consider that surface waves are used in such a daily activity as prey detection, it seems unlikely that any surface-dwelling species has not evolved a ripple signal system. As indicated by Lang's studies on *Notonecta*, it may be that all surface-dwellers are able to distinguish the subtleties of wave patterns produced by various activities of conspecifics as compared to heterospecific surface dwellers, prey species, and various random wave patterns. The question is: How could ripple communication have evolved in the midst of all that environmental noise, particularly in streams? The answer certainly lies in the example of how humans communicate effectively in the midst of a raucous cocktail party. Surface dwellers must have developed filtering capacities to handle noisy wave environments, along with very redundant signals, just as we can understand generally repetitive, predictable comments made at cocktail parties.

One can imagine the evolution of specialized ripple signal communication by selective advantages adding up to ritualized wave production, with concomitant sensory tuning. The initial stages of signal evolution would probably involve short-range, subtle patterns, difficult for a human observer to distinguish from general activity-produced waves. Further studies emphasizing ripple communication or its possibility should take care to look for such subtle patterns,

perhaps to reveal a much greater richness of signal types than appears to exist at present.

Whether it is expressed openly or not, many biologists are drawn to their occupation in part because they gain a sense of beauty from studying living things. The study of ripple communication combines an appreciation of the animals that make the signals and a fascination for the peculiar elastic surface layer of water molecules that is such an important boundary layer for so many life forms — including the life of human imagination and its own reflections.

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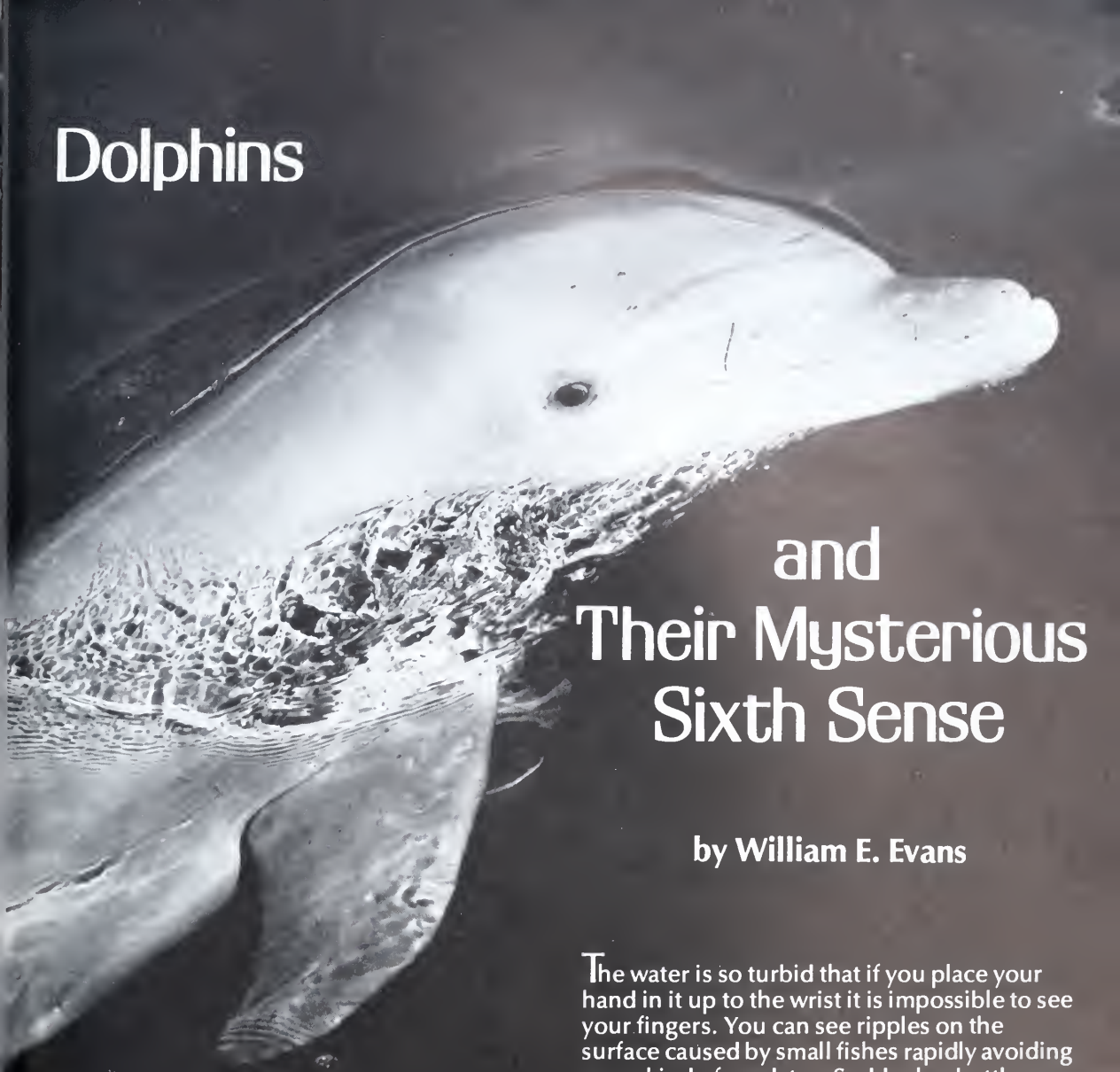
Corrections

In the article by Francisco J. Palacio on "The Development of Marine Science in Latin America," appearing in the last issue of *Oceanus* (Vol. 23, No. 2), the captions to the photos on page 46 were inadvertently reversed. Thus the Argentine Fishing Institute is by the water and the Oceanographic Institute at the University of Sao Paulo is inland.

In the same issue, proper credit was not given for the charts on page 31 of Daniel P.Finn's article on "Georges Bank: The Legal Issues." The charts were adapted from a paper by Malcolm L. Spaulding and Mark Reed in the Ocean Management Program at the University of Rhode Island entitled "A Fishery Oil Spill Interaction Model," 1979 Oil Spill Conference, Los Angeles, California.

Dolphins



and Their Mysterious Sixth Sense

by William E. Evans

The water is so turbid that if you place your hand in it up to the wrist it is impossible to see your fingers. You can see ripples on the surface caused by small fishes rapidly avoiding some kind of predator. Suddenly a bottlenose dolphin leaps clear of the water with a fish in his mouth. How did he catch such an evasive prey without vision? The answer — bottlenose dolphins are echolocaters.

Echolocation is an orientation mechanism based on an animal's ability to detect objects at a distance by listening to the echoes of its own signals. Although echolocation is now generally accepted as one of the many amazing sensory systems that animals use to monitor their environment, its acceptance by the scientific community was slow in coming.

Atlantic bottlenose, Tursiops truncatus. *(Photo by Russ Kinne, PR)*

Early History

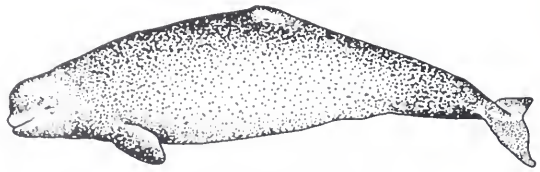
The phenomenon of a sixth sense was first observed in bats by the Italian scientist Lazzaro Spallanzani in 1794. In experiments, bats were able to avoid obstacles even though all their known senses were eliminated. This led Spallanzani and his collaborators to the conclusion that bats had a "sixth sense." In 1798, L. Jurine repeated the experiments with blinded bats and was successful in disorienting his test animals by filling their ears with a waxy substance. He was convinced he had demonstrated the importance of hearing in the bats' amazing orientation and obstacle avoidance behavior. Unfortunately, the French naturalist Georges L. C. F. D. Cuvier, one of the most prestigious scientists of the age, ridiculed the concept, and most research in this domain ceased until the 20th century. By 1920, it was strongly suspected that this orientation capability was acoustic, leading H. Hartridge to suggest a possible kinship between the system by which bats orient themselves and the principle developed by the French physicist Paul Langevin which was used for the acoustic detection of submarines in World War I (see *Oceanus*, Vol. 20, No. 2, 1977, pp. 67-75).

The concept that an animal can examine its sensory environment not only by listening, seeing, smelling, tasting, and touching, but also by probing with self-generated signals, again lay dormant until the late 1930s. In 1938, G. W. Pierce and Donald Griffin at Harvard University used specialized listening equipment to demonstrate that bats emit ultrasonic signals. Following this discovery, Griffin, in collaboration with Robert Galambos (also of Harvard University), carefully repeated all of the previous experiments and concluded that: nothing stops a bat from avoiding obstacles except loss of hearing and voice; bats emit ultrasonic signals in flight, and they can hear these emissions; and bats hear the echoes of the ultrasonic sounds they emit and orient themselves accordingly. Even armed with the results of these very elegant experiments, scientists did not wholeheartedly accept the concept.

There was another problem. Radar and sonar, and the bats' system was certainly sonar, were still highly classified developments in military technology. The idea that animals might have a system even remotely similar to man's brilliant achievements in electrical engineering struck many as sheer heresy. It was partly to overcome this resistance that Griffin suggested the term *echolocation*, which, now that the earlier stigma and secrecy have been removed, is used synonymously with the term *animal sonar*.

Echolocation Underwater

It is interesting that Hartridge's comparison of bat orientation and submarine sonar did not lead to



White Whale, Beluga (Delphinapterus leucas).

investigation of acoustic detection in marine organisms. Sound emissions from whales, dolphins, and porpoises had been observed for centuries. Anecdotes about the ability of porpoises to navigate, avoid obstacles, and catch fishes were common among fishermen.

In 1947, Arthur F. McBride, curator of Marine Studios (later Marineland of Florida), recorded some porpoise (*Tursiops truncatus*) behavior suggesting these animals might have a highly specialized mechanism for learning about their environment through sound. His observations were made while trying to capture bottlenose porpoises in turbid water, usually at night. McBride noted that the animals avoided a fine-mesh net, but did not avoid a 10-inch, coarse-mesh net (which has less acoustic reflectivity). Furthermore, they immediately went over the net when, momentarily, the cork line was pulled below the surface by others striking the net from below. The possibility that the animals were guided by bioluminescence was considered, but no bioluminescence was visible. McBride, reminded of the sonic sending and receiving apparatus which enables bats to avoid obstacles in the dark, put together the complex development of the dolphin's brain with the importance of the dolphin's acoustic sense. This was the first direct inference backed by good evidence that dolphins use sound in navigation.

Well before McBride's observations became known, some workers had suspected that cetaceans (the whale family) could echolocate. The first rather crude experiments to determine the hearing range of the Atlantic bottlenose revealed that these animals could respond to ultrasonic frequencies. The turbid coastal waters inhabited by *Tursiops truncatus* suggested that this species and others might well use echolocation in food-finding and navigation. In 1953, however, William Schevill of the Woods Hole Oceanographic Institution and Barbara Lawrence of the Harvard Museum of Comparative Zoology, in an auditory response experiment with a dolphin in near-opaque waters, listened for echolocation signals but heard none. To them, the question remained open.

Suspicions Verified

When F. G. Wood arrived at Marineland of Florida as curator in 1951, he found that his predecessor McBride had acquired a U.S. Navy underwater sound projector. Using this as a hydrophone, together with an amplifier, tape recorder, and speaker or headset, he began to record and listen to

the sounds produced by the bottlenose dolphins and, usually, one or two spotted dolphins, *Stenella plagiodon*, maintained in a large tank. The hydrophone was suspended in front of a porthole so that the experimenter could, while listening, record notes about the behavior of the animals. Wood found that whenever the transducer was hung in the tank, the dolphins exhibited their normal curiosity about strange objects or new introductions. As they swam within a few feet of the transducer, they would peer at it and at the same time emit rasping and grating sounds. Wood suggested that they were "echo-investigating" the hydrophone. The animals gave the same response when presented with other objects, such as a bucket or length of pipe. In retrospect, it seems that although the animals could see the object clearly, they also relied on the different kinds of information received from the echoes of their sound emissions.

Later experiments in the 1950s by Schevill and others removed doubt that the Atlantic bottlenose had sonar, although vision was not completely excluded. Positive evidence was provided by K. S. Norris of the University of California at Santa Cruz, who successfully blindfolded a porpoise by covering its eyes with latex suction cups. The trained Atlantic bottlenose swam normally when blindfolded and avoided obstacles, including pipes suspended vertically to form a maze. The porpoise oriented to fragments of fish tossed in the water and took them as they drifted downward. Norris noted that when a bit of food drifted below the level of the melon,* the animal did not respond to it. He speculated that the sounds were directional and being projected from the melon.

During the same period, Wood was also attempting to devise a blindfold for dolphins, albeit unsuccessfully. Hearing of Norris's success using suction cups, Wood used the same technique to blindfold a recently caught, untrained *Tursiops truncatus*, taken from turbid inshore waters. Once the suction cups were in place, the porpoise swam about the tank with no indication that it lacked vision. It went directly to fishes tossed in the water, taking them as they drifted down.

Norris, in 1969, described porpoises taken from clear oceanic waters that had become disoriented when unable to use vision. In one experiment, a *Tursiops truncatus* captured in Hawaiian waters was taught to push a paddle on command. After being blindfolded, the animal failed to find the paddle despite the fact that it was 20 centimeters in diameter and covered with acoustically reflective foam.

Norris concluded that echolocation behavior in marine mammals very likely includes a great deal of learning. Animals living in clear seas may use their systems in ways quite different from those inhabiting turbid inshore waters.

*The round mass of blubber between the blowhole and the end of the nose in several cetaceans.

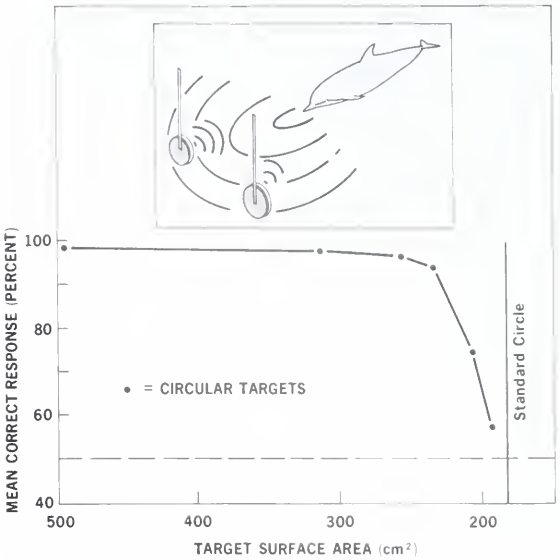


Figure 1. A bottlenose dolphin's discrimination performance on target disks of various surface areas against a standard circle of 180 square centimeters (percentage of correct responses).

The Adaptiveness of Porpoise Echolocation

Observations in the 1950s confirmed the existence of porpoise echolocation and provided some insight into its adaptive features. The work that followed in the 1960s concentrated on refining knowledge of the effectiveness and complexity of this remarkable sensory specialization.

It was experimentally demonstrated that blindfolded Atlantic bottlenoses not only can detect, avoid, and find objects, but also can discriminate differences in targets that affect their acoustic reflectivity — that is, size, shape, and mass (density) (Figures 1, 2, and 3). During the same period it was shown that the harbor porpoise, *Phocoena phocoena*, is also an echolocater.

An international conference on biosonar was held in Frascati, Italy, in 1966, where scientists raised significant questions that were to shape some of the research that followed. The sophisticated sensory capabilities of porpoises were impressive, but how important were they in navigation or food finding? What acoustic information was being used by the animals? The bottlenose and harbor porpoises inhabit inshore waters and even rivers where the water is murky and sometimes full of suspended debris that could represent false targets and navigational hazards. Did open-sea species, such as the common dolphin and pilot whale, echolocate? Short-duration clicks had been heard from all toothed whales recorded, but although

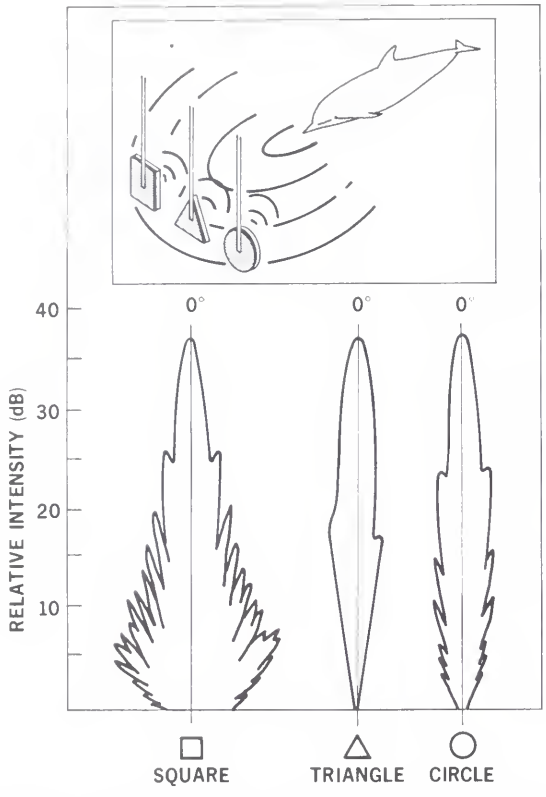


Figure 2. Radiation patterns of dolphin echolocation pulse echoes from square, triangular, and circular targets of the same target strength (reflectivity). The test animal, a bottlenose dolphin, correctly selected the standard target (circular plate) in 90 percent of the trials.

many authors referred to these acoustic emissions as echolocation clicks, they were not evidence of an echolocation capability.

By 1973, the literature had increased immensely. The number of species for which an echolocation capability had been demonstrated experimentally was growing. Amplitude and frequency content of the pulses (clicks) used were being measured with increasing accuracy, and signal processing techniques were being employed to gain a greater understanding of the total delphinid sonar system.

In 1967, the cetacean species known to use echolocation were *Phocoena phocoena* and *Tursiops truncatus*. By 1973, several more species had been added to this list. Studies of the Amazonian freshwater dolphin *Inia geoffrensis* (Figure 4) indicated that this species could discriminate the difference in diameter of thin wires presented as pairs behind a visually opaque, acoustically transparent screen. The common dolphin, *Delphinus delphis*, could detect differences in complex geometric figures as well as *Tursiops truncatus* could. A preliminary study was done with a Pacific pilot whale, *Globicephala*, trained to wear latex eye cups and retrieve rings thrown into the water. A Pacific whitesided dolphin, *Lagenorhynchus obliquidens*, learned to avoid obstacles without the aid of vision. When blindfolded, this species could detect differences in

Figure 3. Echolocation "run" of a blindfolded bottlenose dolphin on a pair of metal disc targets. The standard or "correct" target is on the animal's right.

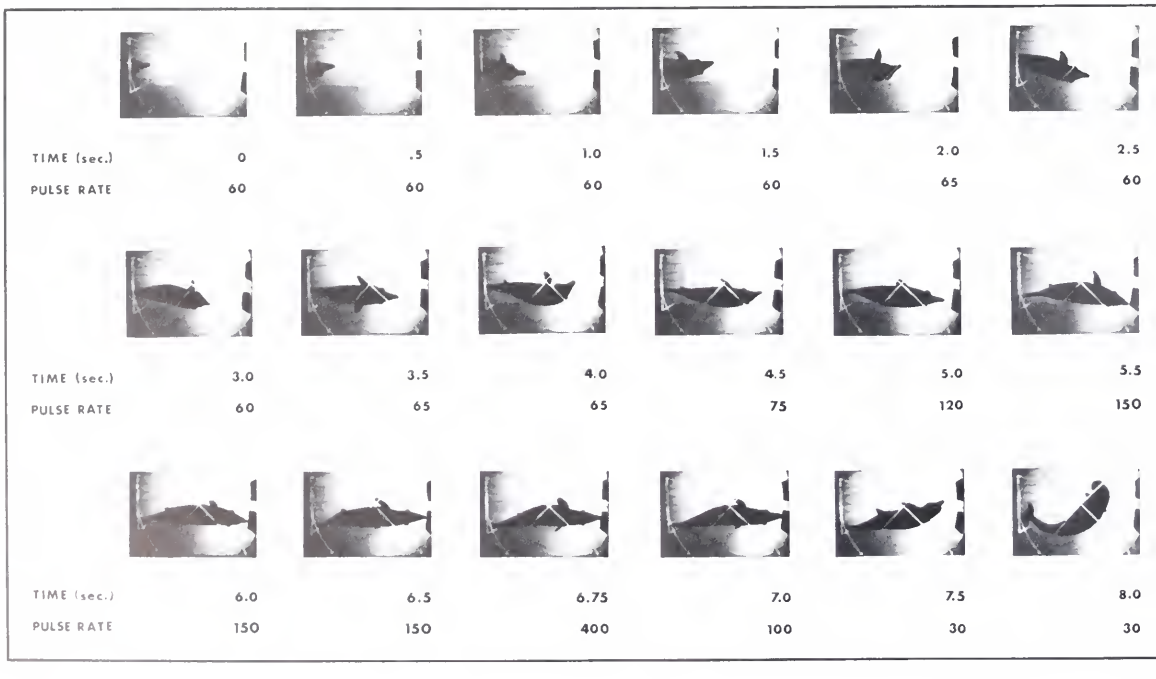


Figure 4. Amazon River dolphins, Inia geoffrensis. *(Photo courtesy of Naval Missile Center, Point Mugu, California)*

plates of the same thickness but made from different metals, with the same accuracy as the bottlenose. During a study designed to determine hearing thresholds, a captive killer whale, *Orcinus orca*, was also trained to retrieve a ring while blindfolded.

Instrumentation was becoming more sophisticated. The total recording system of hydrophones, associated amplifiers, and tape recorders had much broader responses, now 100 Hertz to 120 kilohertz typically, compared with the 50 Hertz to 20 kilohertz of the last two decades. More information on frequency and waveform characteristics of the pulse was available, but it required increasingly complex interpretation.

Researchers raised questions on the adaptive nature of the finely tuned echolocation of various small toothed whale species. Odontocetes (the small toothed whales) inhabit very diverse aquatic environments, from rivers and lakes to estuaries, open seas, and fjords. The frequency contents of their pulses seem to reflect adaptation to these environments. For example, the harbor porpoise, Amazon River dolphin, and beluga whale (Figure 5) generally produce pulses with low-frequency components, but when they are echolocating under conditions of poor or no visibility, their pulses contain considerable energy in the ultrasonic range. These species, as well as the Indus River dolphin, *Platanista indi*, which has a similar echolocation pulse, inhabit turbid waters, feed on very small prey, and frequently must distinguish their prey from drifting debris.

Scylla

In 1969, K. J. Diercks, from the University of Texas, and the author conducted a series of echolocation discrimination tests with a female Atlantic bottlenose named Scylla. We decided to test her efficiency, while blindfolded, in catching a live,

Figure 5. A beluga whale stationing at an acoustically treated experimental station during an echolocation and underwater hearing study conducted at Sea World, San Diego.

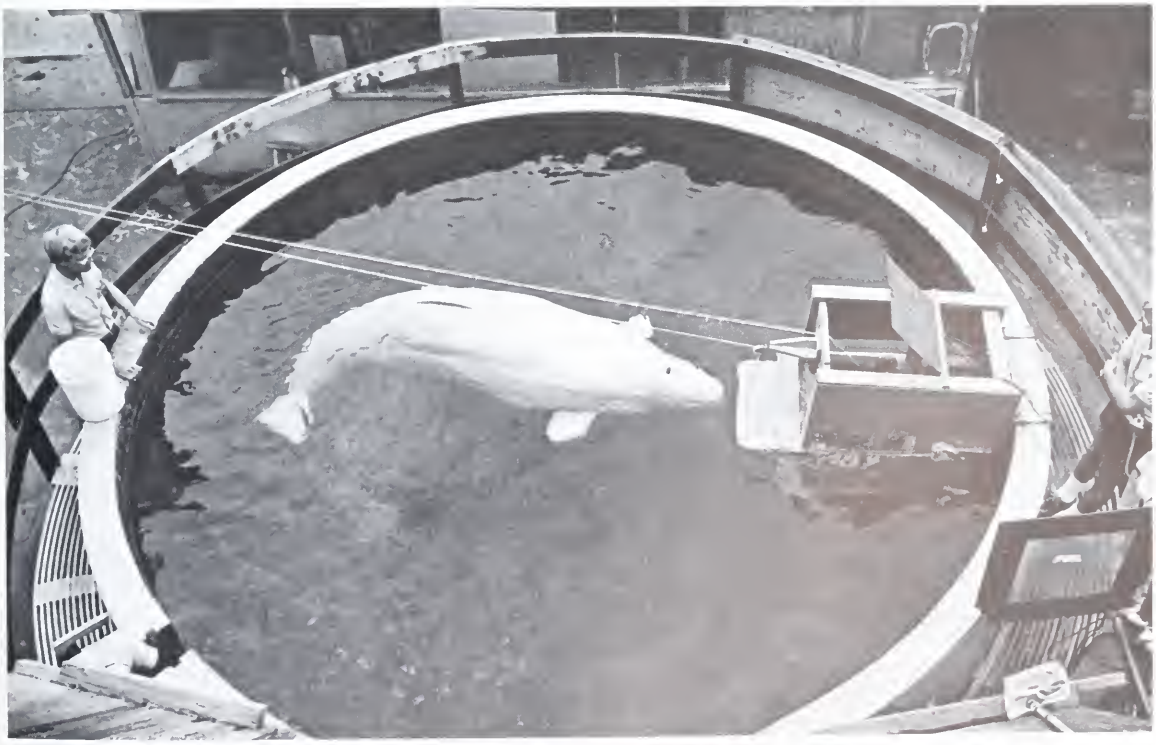


Figure 6. Scylla, with broadband hydrophones attached to her melon and rostrum. The method of attachment and configuration is similar to the one used in the live fish study. This was a pre-test training run.

free-swimming fish. The bottlenose was fitted with seven broadband hydrophones (Figure 6). Five of the hydrophones were directed inward to monitor the transmitted echolocation signals, and two, attached to the blindfolding eyecups, were directed forward to detect target echo signals. The seven hydrophones were connected through an umbilical (a cable) to poolside preamplifiers and magnetic tape recorders. In addition, two broadband hydrophones were positioned in front of the two targets and a third hydrophone was located behind the target plane, all three connected via amplifiers to tape recorders. The movements of the dolphin were monitored by two video cameras, one above the pool and one underwater.

The monitoring hydrophones detected echolocation signals during all discrimination trials prior to the live fish experiment. In the trial right before the fish was introduced, a metal sphere and a dead fish suspended by its tail were used as targets. Then a metal sphere was suspended at the left-hand target site to maintain the semblance of a routine echolocation trial. As Scylla approached, emitting echolocation clicks, a live fish, something she had not encountered during her several years in captivity, was dropped into the water at the right-hand target location.

The porpoise, without emitting any detectable echolocation signals, positioned herself adjacent to the fish. She maintained this position with respect to the fish as it swam around the perimeter of the pool. *No* echolocation signals were detected by any of the ten hydrophones during this circuit. When the fish reached the nylon net suspended in the passage connecting the two pools, it darted through. Scylla rolled and became entangled in the hydrophone umbilical. She was then held at the side of the pool while all of the attached hydrophones and the two eyecups were removed. When released, she turned to the nylon net where she could now see the fish in the adjacent pool. She began to emit clicks at rates as high as 1,500 per second. The repetition rate reached a level that she apparently was unable to maintain; her head would jerk, she would stop emitting, then begin again until the next head jerk, and so on. Subsequently, the fish was netted and tossed back into the test pool where Scylla, again blindfolded, now caught it and returned it to her trainer — all without emitting a detectable sound. This was repeated four more times, with the fish returned dead after the fifth retrieval. It was then hand-fed to her, and she readily ate it.

This experiment is described in some detail because it is probably unique in its circumstances and it appears to be significant. We can only surmise that passively received acoustic information enabled the blindfolded porpoise to track the fish. Since she made no attempt to catch the fish during a complete circuit of the tank, though she later retrieved it five times, we can also assume that she did not consider the live fish as a food object. Scylla's performance indicated that these animals are able to detect, track, and catch fishes without using echolocation or vision. This mode of acoustic behavior may be more commonly used in nature than we suspect.

Scylla's vocal behavior and head jerks when she could see the fish in the other pool but not get at it because of the net may be explained as an emotional outburst. Long-term observations of several common dolphins strongly suggest that click-train emissions often occur in social contexts and represent emotional and perhaps communicative behavior.

We can view cetacean echolocation as having three primary functions: sound production, echo reception, and acoustic echo processing. However, as we can see from the experiment just described, echolocation must not be viewed as distinct from another acoustic capability — receiving and interpreting other sounds in the environment. This poses problems in our investigations, since our perception of the world is inherently limited by our particular ensemble of sensory equipment. We cannot know, or even imagine, the perceptual world of other animals that differ markedly from us in sensory capabilities. Using behavioral or electrophysiological techniques, we can experimentally "ask questions" of animals and obtain certain information regarding their sensory threshold ranges and apparent limitations. But we cannot know the complete realm of their perception and how that perception is adapted to the environment in which they live.

Still other aspects of sound production in dolphins and porpoises that apparently cannot be viewed as completely distinct from echolocation are those having to do with emotional state (as seems to be demonstrated by the live fish experiment) and communication. It has commonly been thought that clicks are echolocation signals, whereas whistles and other vocalizations are the ones that have communicative or emotional significance. However, there is growing evidence that clicks may serve other purposes. William Watkins, of the Woods Hole Oceanographic Institution, while not precluding the use of sperm whale clicks for echo information, found evidence that clicks are used as communication signals (see *Oceanus*, 1977, Vol. 20, No. 2, pp. 50-58).

Audition and the Dolphin Brain

Basic to the echolocation capability of porpoises is neuroprocessing — the integration, analysis, and interpretation of acoustic information contained in the echoes. Neuroprocessing requires neural tissue. It is well known that all porpoises have very impressive brains. Although there is much variation in the size of toothed whale brains, in general they are characterized by large size, with greater width and height than length, substantial development of the cerebral hemispheres, and intricate convolutions of the cortex.

If we accept the idea that the mass of brain tissue controlling a particular function is appropriate to the amount of information processing involved in performing the function, we could hypothesize that the great brain size of toothed whales to some extent reflects their known and presumed acoustic attributes. Another possibility is that these animals — at least those with the largest brains — possess an intelligence comparable to that of the only other mammals with a structurally and functionally similar brain — apes and humans. But, as J. C. Lilly says, "convincing scientific evidence of cetacean intelligence remains to be established, and arguments comparing levels of human and dolphin [intelligence] are philosophical, not scientific" (1978).

Although echolocation would seem to have a high adaptive value for an aquatic vertebrate, there is hardly any evidence that it has evolved in marine animals other than toothed whales. The sea catfish, *Arius felis*, has been shown by William Tavolga of the Mote Marine Laboratory in Sarasota, Florida to have a rudimentary acoustic orienting capability. The late Thomas Poulter, then of the Stanford Research Institute in California, suggested echolocation in pinnipeds (such as seals and walruses) and penguins. But attempts to experimentally demonstrate such an ability in pinnipeds have been unsuccessful, and penguins have not been studied in this respect. It is possible that an echolocation capability will be found in some of the Pinnipedia. The Weddell seal, for instance, which lives on the fast, or permanent, ice in the Antarctic, has a need to feed in total darkness and find breathing holes, and has an underwater repertoire of at least 35 calls. At present, however, there is no indication of the existence of a complex aquatic biosonar system other than in dolphins and porpoises. Other aquatic vertebrates seem to have taken the path of different sensory systems or combinations of systems.

Even those species which have demonstrated a highly developed sonar capability may use it less than we assume, as the experiment with Scylla showed. Every year a large number of dolphins and porpoises, including species known to have an excellent sonar system, become entrapped in gill nets, purse seines, and nets set off South African beaches to protect bathers from sharks. The target strength of at least some of these nets should make them readily detectable. Such entrapments may result from a porpoise's inattention or its concentration on pursuing prey. Still, we have no idea how much of the remarkable detection and discrimination capability of these animals is used in their natural habitats and how much of it is an untapped capacity brought out by a selection process — training.

William E. Evans is a biologist. Since 1977, he has been Director of the Hubbs-Sea World Research Institute in San Diego, California, and Orlando, Florida. Prior to that he was a Senior Research Biologist for the United States Navy. He has been studying dolphin and porpoise communication and echolocation since 1959.

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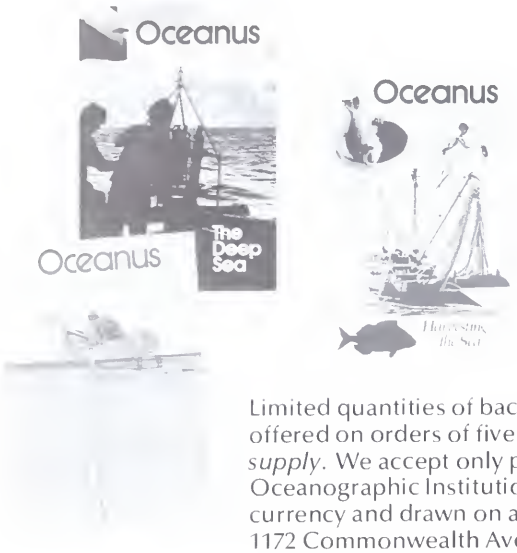

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THE DEEP SEA, Vol. 21: 1, Winter 1978 — Over the last decade, scientists have become increasingly interested in the deep waters and sediments of the abyss. Articles in this issue discuss manganese nodules, the rain of particles from surface waters, sediment transport, population dynamics, mixing of sediments by organisms, deep-sea microbiology — and the possible threat to freedom of this kind of research posed by international negotiations.

MARINE MAMMALS, Vol. 21:2, Spring 1978 — Attitudes toward marine mammals are changing worldwide. This phenomenon is appraised in the issue along with articles on the bowhead whale, the sea otter's interaction with man, behavioral aspects of the tuna/porpoise problem, strandings, a radio tag for big whales, and strategies for protecting habitats.

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OCEANS AND CLIMATE, Vol. 21:4, Fall 1978 — This issue examines how the oceans interact with the atmosphere to affect our climate. Articles deal with the numerous problems involved in climate research, the El Niño phenomenon, past ice ages, how the ocean heat balance is determined, and the roles of carbon dioxide, ocean temperatures, and sea ice.

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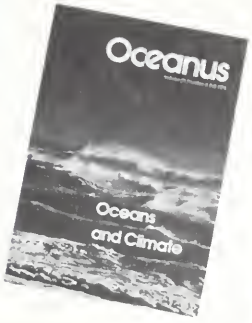

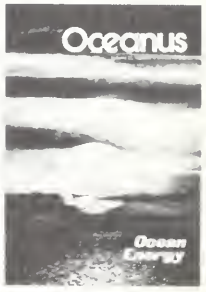

HARVESTING THE SEA, Vol. 22:1, Spring 1979 — Although there will be two billion more mouths to feed in the year 2000, it is doubtful that the global fish harvest will increase much beyond present yields. Nevertheless, third world countries are looking to more accessible vessel and fishery technology to meet their protein needs. These topics and others — the effects of the new law of the sea regime, postharvest fish losses, long-range fisheries, and krill harvesting — are discussed in this issue. Also included are articles on aquaculture in China, the dangers of introducing exotic species into aquatic ecosystems, and cultural deterrents to eating fish.

GENERAL ISSUE, Vol. 22:2, Summer 1979 — This issue features a report by a group of eminent marine biologists on their recent deep-sea discoveries of hitherto unknown forms of life in the Galápagos Rift area. Another article discusses how scuba diving is revolutionizing the world of plankton biology. Also included are pieces on fish schooling, coastal mixing processes, chlorine in the marine environment, drugs from the sea, and Mexico's shrimp industry.

OCEAN/CONTINENT BOUNDARIES, Vol. 22:3, Fall 1979 — Continental margins are no longer being studied for plate tectonics data alone, but are being analyzed in terms of oil and gas prospects. Articles deal with present hydrocarbon assessments, ancient sea-level changes that bear on petroleum formations, and a close-up of the geology of the North Atlantic, a current frontier of hydrocarbon exploration. Other topics include ophiolites, subduction zones, earthquakes, and the formation of a new ocean, the Red Sea.

OCEAN ENERGY, Vol. 22:4, Winter 1979/80 — How much new energy can the oceans supply as conventional resources diminish? The authors in this issue say a great deal, but that most options — thermal and salinity gradients, currents, wind, waves, biomass, and tides — are long-term prospects with important social ramifications.

A DECADE OF BIG OCEAN SCIENCE, Vol. 23:1, Spring 1980 — As it has in other major branches of research, big science has become a powerful force in oceanography. The International Decade of Ocean Exploration is the case study. Eight articles examine scientific advances, management problems, political negotiations, and the attitudes of oceanographers toward the team approach.

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